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Fisheries Research Bulletin No. 11

Biology and Distribution of the Toheroa, *Paphies (Mesodesma) ventricosa* (Gray)

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By
P. Redfearn

Fisheries Research Division
New Zealand Ministry of Agriculture and Fisheries

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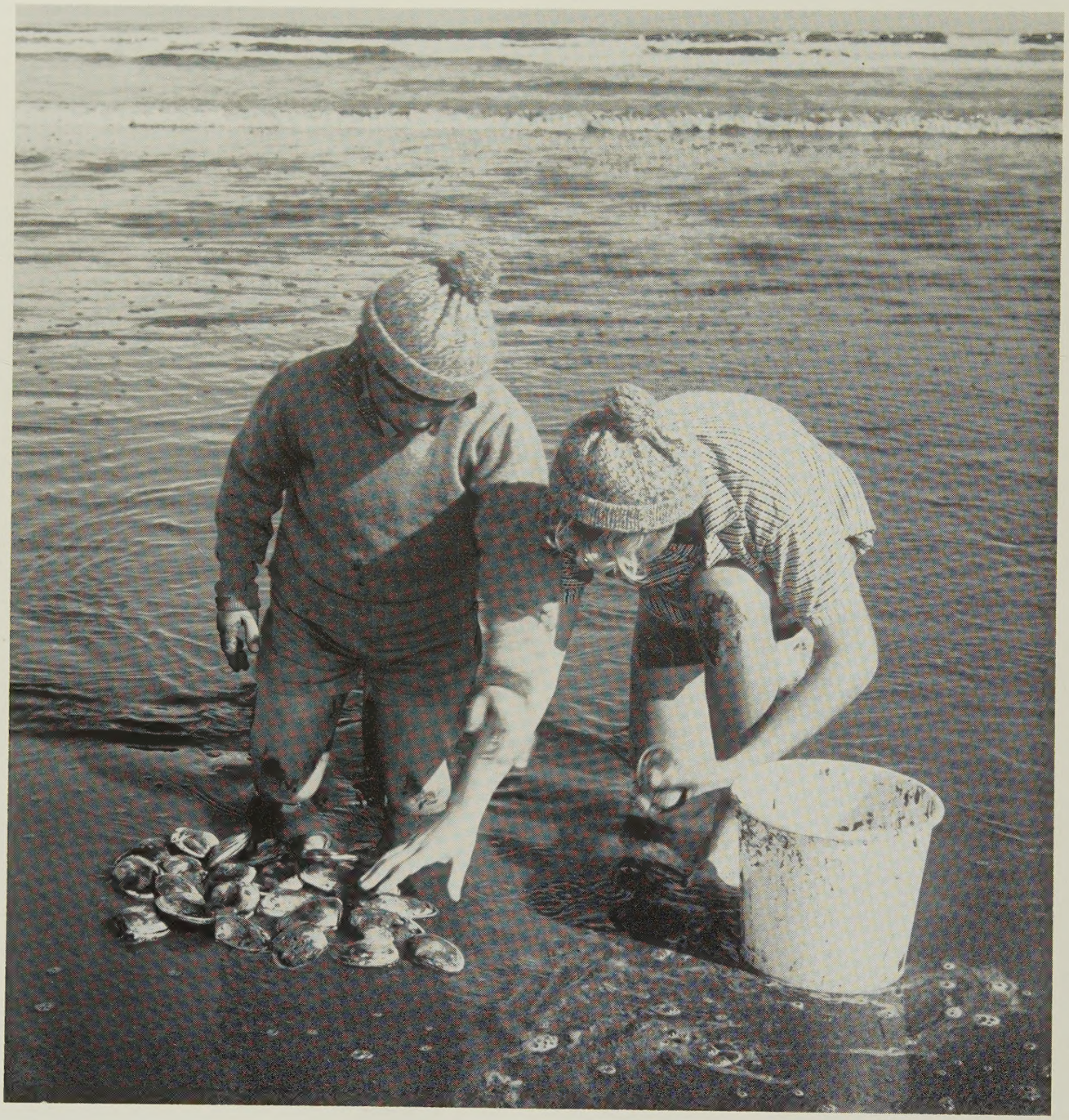

[National Publicity Studios photograph

Frontispiece: The toheroa is a national delicacy and partly because of its popularity its population has declined in recent years.

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By
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Ministry of Agriculture
and Fisheries, Wellington

Fisheries Research Division
New Zealand Ministry of Agriculture and Fisheries
1974

Published by the New Zealand Ministry of Agriculture and Fisheries
Wellington
1974

This series of research bulletins, which was begun in 1968, was formerly published by the New Zealand Marine Department before the Fisheries Research Division was transferred from that Department to the Ministry of Agriculture and Fisheries in September 1972.

FOREWORD

AS a unique delicacy the toheroa has a special appeal for New Zealanders and there is a natural desire that it should be harvested regularly and in quantity. Wide fluctuations in population density have been variously attributed to overfishing, damage by vehicles, etc., but it is now established that the principal factors influencing the populations are environmental and biological. Under the right conditions rapid repopulation can occur even when stocks are low.

It is also apparent that direct augmentation of the populations in the very extensive surf beaches would be extremely difficult. At present, because of the very high natural mortality, there is considerable wastage of the resource, and this study points to the need for a review of the current conservation measures.

It is a pleasure to record thanks to Mr J. K. Shea and Meredith Bros. and Company Ltd., of Auckland, whose fellowship made it possible for this work to be undertaken by Mr Redfearn. This is the first occasion when industry has contributed directly to a Government scientific study of one of our fisheries.

G. DUNCAN WAUGH,
Director, Fisheries Research Division.

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INTRODUCTION

TOHEROA is a Maori name now used exclusively for the large bivalve molluscs belonging to the Mesodesmatidae that inhabit sand beaches mainly on the west coast of New Zealand. The shell is solid and ovately wedge shaped (Fig. 1). The valves do not close completely and the gaps formed are covered by folds of the mantle. The siphons are separate and highly contractile. The outer aperture of the inhalant siphon is encircled by a complex of tentacles which serves to prevent the passage of large particles into the mantle cavity. Wade (1969) indicated similar tentacles on *Donax denticulatus* Linnaeus and has shown that they filtered out particles larger than 250 μm. The foot is large and triangular and enables the animal to burrow rapidly into the sand.

The distribution of toheroa is restricted to the mainland of New Zealand and they are most abundant on the west coast of the North Island on Ninety Mile, Dargaville*, and Muriwai Beaches (Fig. 2). They are active burrowers and may be found some 20 cm below the surface of exposed fine sand beaches, where they often aggregate into beds at the mean tide level.

Shellfish were apparently an important aspect of the diet of the Maori in the pre-European era. Davidson (1967) has reviewed the literature on midden analysis in New Zealand, and molluscan shell remains constituted a large part of these middens. Stallworthy (1916) noted: "The toheroa beds on the West Coast beach are said to have been a valuable source of food supply in the olden times, and it is thought that it was probably the attempts to secure the possession of these beds that gave rise to many of the old wars among the natives." By 1900 the European population had also learnt to appreciate the mollusc, and a small fishery for it had been started. Since then the fishery has changed from a Maori food source and commercial venture to a major recreational or amateur fishery. The toheroa is now a national delicacy, and thousands of people gather it during the open seasons. Partly because of its increasing popularity there has been a decline in the toheroa population.

Fig. 1: Toheroa, *Paphies (Mesodesma) ventricosa.*

Hoby (1933) presented a thesis on the anatomy of *Amphidesma ventricosum* Gray, and Rapson (1952, 1954) made a general ecological study of the animal. Rapson also suggested some methods of controlling the fishery to produce more stable stocks. Cassie (1951, 1955) examined the population structure and postulated that part of the population was in the sub-littoral. Waugh and Greenway (1967) offered tentative evidence in support of this theory. Dawson (1954) made a study of the population structure of a related species, the tuatua. Dawson (1954, 1959) also discussed the nomenclature of the family. Beu (1971a, 1971b) has reviewed the nomenclature of the genera of the Mesodesmatidae and has commented on some of the Australasian species.

These studies left questions unanswered in the fields of growth, reproduction, and the possible mass migration of toheroa and did not explain the reasons for aggregation into beds. The major fluctuations in the beach populations in recent years have also pointed to the need to ensure adequate protection for the beach stocks against the chances of overexploitation.

For these reasons Meredith Bros. and Company Ltd., of Auckland, who have a concession to gather the shellfish commercially on the southern end of Dargaville beach, offered to finance a study to further our knowledge of the toheroa.

* The name Dargaville beach is now commonly used to denote the stretch of beach between North Kaipara Head and Maunganui Bluff. The beach was previously known as the North Kaipara beach and is referred to as such by Rapson (1952) and in early Marine Department Annual Reports.

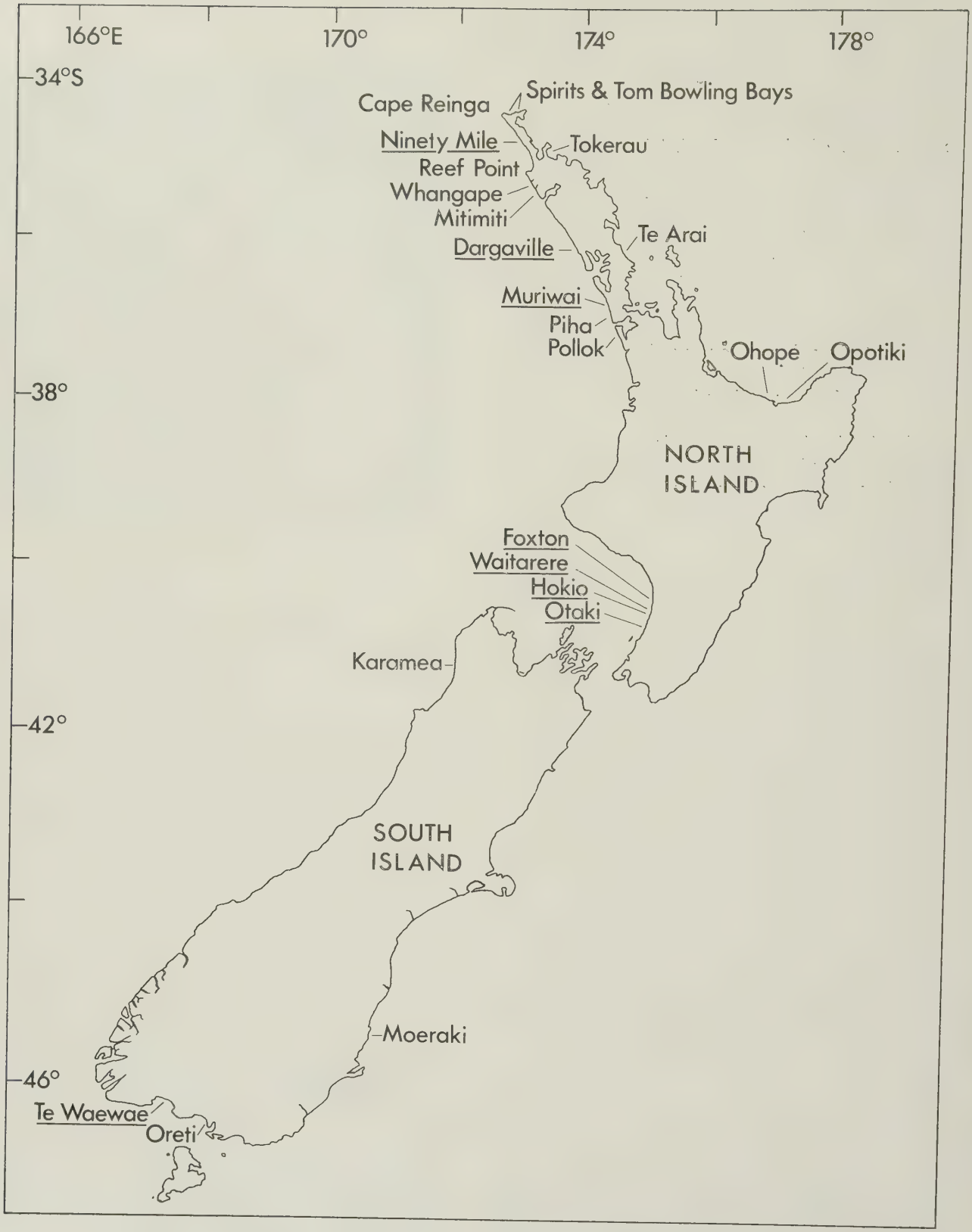


Fig. 2: Distribution of toheroa in New Zealand. Major population sites are underlined.

MATERIALS AND METHODS

In collaboration with Meredith Bros. and Company Ltd. and the former New Zealand Marine Department* it was decided that most of the experimental work would be carried out on the southern half of Dargaville beach within the concession area (Fig. 3). A 5-mile (8-km) section was closed to the public so that comparisons between exploited and unexploited populations could be made. Unfortunately this aspect of the work was nullified somewhat by the nefarious activities of poachers.

BEACH MEASUREMENTS

Meredith Bros. have set marker posts into the dunes backing the littoral† at ½-mile (800-m) intervals. These marker posts were used as reference points for horizontal measurements along the beach. Distances under 800 m were measured either by pacing (1 pace = about 80 cm) or with a metre tape. These marker posts were numbered from 1 to 33 to designate the different sections in the concession.

Beach profiles were first measured with a tacheometric theodolite, but for most of the profiles a simple technique described by Emery (1961) was used. In this method two graduated 1.5-m poles were held vertically a known horizontal distance apart at right angles to the tide front. The difference in elevation between the poles was measured by aligning the top of the seaward pole with the horizon and a point on the landward pole. The distance down the landward pole of the interception point was the difference in elevation.

As it was impracticable to correct the levels derived for any one profile to the ordnance datum, they were corrected approximately to chart datum. During the first survey at a station the elevation of the tide front was calculated from the tidal data for the day of the survey. The level of a fixed point on the station marker post was interpolated from this elevation, and all subsequent profile levels were established with reference to this point. Though profiles established in this way could not be compared from station to station, changes in level at any one station were real.

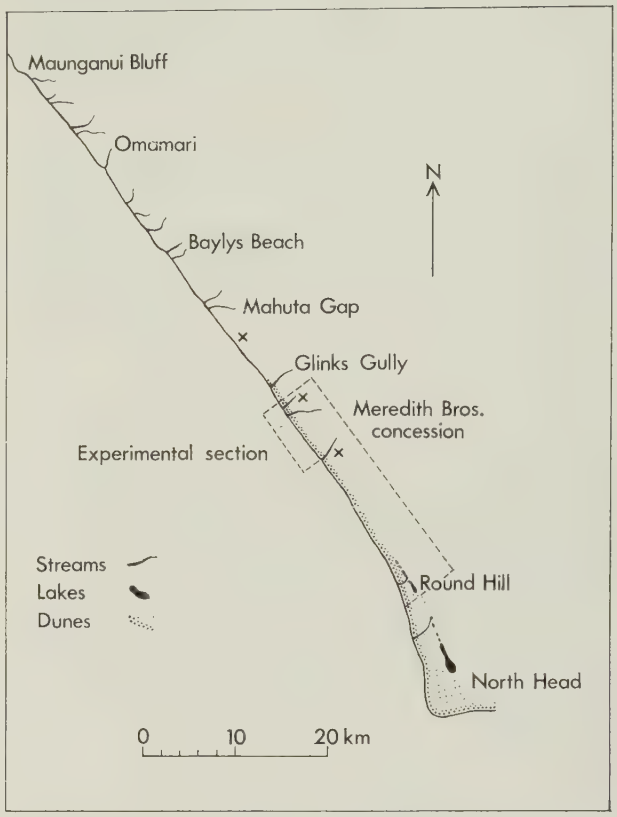


Fig. 3: Dargaville beach, showing the location of the experimental area and the major freshwater streams. Profile stations are indicated by crosses.

POPULATION CENSUS AND STRUCTURE

Census and population structure data used in this bulletin have been obtained from three sets of surveys—Marine Department, Meredith Bros., and the author's.

Marine Department Surveys

Only occasional surveys were made before 1962, but annual or biennial surveys have since been conducted on the principal beaches in the North Auckland Peninsula, the Wellington district, and the South Island.

Random transects have been dug across the beach at right angles to the tide front so that they included the whole population. Standard quadrats—2.25 sq ft (0.21 sq m) in Northland and 0.5 sq m in the South Island—were dug at equally spaced intervals along each transect or a trench was dug. All the toheroa collected in the transect were then sorted into size groups and counted. The method used to select the transect stations varies from region

* The Fisheries Research Division was formerly a division of the New Zealand Marine Department. As from 1 September 1972 the division became part of the New Zealand Ministry of Agriculture and Fisheries, and the Marine Department was disbanded.

† The term littoral in this bulletin means that area of beach between the levels of mean extreme high water springs and mean extreme low water springs, a vertical interval of some 2.9 m.

to region, but all are random in that they do not differentiate between isolated and aggregated groups of toheroa. Greenway (1969) described the system used on the North Auckland Peninsula, Williamson (1969a) that used in the Wellington district, and Street (1971) that used in the South Island.

Meredith Bros. Surveys

Meredith Bros. have also conducted annual surveys of the toheroa stocks on their concession since 1962. The concession has been surveyed in 800-m sections conforming to marker posts. In the survey isolated (non-bed) and aggregated (bed) toheroa are recorded as follows:

Quadrats (4 sq ft, 0.37 sq m) are dug along the beach parallel to the tide front at the mean tide level at 90-pace (about 72-m) intervals until a bed is reached. Beds are surveyed by digging equally spaced quadrats (5 paces, about 4-m intervals) across the aggregation at right angles to the tide front to encompass the population. These transects are repeated along the bed at 45-pace (about 36-m) intervals. The transect intervals are adjusted on small beds to give a reasonable cover.

Toheroa collected from each quadrat are sorted into size groups and counted. In each section the bed populations have been calculated from the mean number of toheroa per quadrat and the bed area. The off-bed population has been calculated similarly. The off-bed area is calculated from the mean bed width by multiplying by 800 m and subtracting the combined lengths of the beds in that section.

Author's Bed Surveys

Selected beds in the closed section were surveyed at about monthly intervals for about 8 months. Datum points were established in the dunes backing the beach and all linear distances measured from the bed site were referred back to these points. Randomly selected transects were dug along the beach at right angles to the wave front to encompass the bed population. Quadrats (0.37 sq m) were dug along the transects at about 4-m intervals. The bed area was calculated by the application of Simpson's rule for irregular shapes. The toheroa from each quadrat were sorted into 0.25-cm length groups and counted. Population estimates were calculated from the mean number of toheroa per quadrat and the bed area.

COLLECTION AND TREATMENT OF THE FLORA AND FAUNA

Regular samples of toheroa were collected from the closed section of the beach for condition analysis and histological purposes. Toheroa were also collected from other parts of the beach at irregular intervals for comparison.

Plankton samples for qualitative purposes were collected at about monthly intervals by hand towing a small conical net through the surf. The net had a mouth area of about 850 sq cm and a mesh size of 150–1,000 μm.

Tissues for histological purposes were preserved in sea water Bouin's fluid and plankton samples in 4% neutralised formalin.

SHELL MEASUREMENT AND AGE DETERMINATION

All linear measurements of the shell were made with either vernier calipers or a measuring board. The latter was similar to that described by Cassie (1955). Shell measurements were made after the pattern established by Loosanoff and Nomejko (1949):

(a) The length of the shell is the greatest measurement approximately parallel with the hinge.
(b) The width of the shell is the greatest measurement at right angles to the length and at right angles to the axis of the hinge.
(c) The depth of the shell is the greatest measurement at right angles to the plane of the above two measurements.

All volumes were measured by water displacement (see Baird 1958).

Cassie (1955) observed that the light and dark bands visible in a toheroa shell when it is viewed with transmitted light were of annual occurrence. He also established that the light bands represented summer growth and the dark bands winter growth. In younger toheroa the light bands tend to be relatively broader, but there is more or less continuous growth throughout the year.

Besides being able to be aged each toheroa shell carries a record of its past growth. From this the length of the shell at each successive year can be measured with a fair degree of accuracy. This process was referred to by Cassie (1955) as shell reading.

SHELL MARKING

During the experimental period some 6,000 toheroa were marked and replanted on the beach. The shells were air dried and painted with Dulux Blue Sealer 581-2571, supplied by Imperial Chemical Industries (N.Z.) Limited. The paint is normally supplied only in blue, but samples of five primary colours were provided on request. Half of the toheroa were measured and marked with a number and the rest were marked with a cross. Some animals were recovered over 1 year after marking and though the paint was considerably sand scoured, the numbers were still legible on most shells.

TAXONOMY AND DISTRIBUTION

TAXONOMY

Toheroa belong to a group of large mactracean bivalves living on New Zealand sand beaches. These bivalves have been known for many years by the generic name *Amphidesma,* but Dawson (1959) showed that it could not be used for this group of molluscs in New Zealand, since the genus *Amphidesma* Lamarck, 1818, belongs to the family Semelidae Stoliczka, 1870, and the New Zealand mactracean bivalves belong to the family Mesodesmatidae Gray, 1840. He concluded that the name *Donacilla* de Blainville, 1819, should be used instead of *Amphidesma* and that this generic name should be used for the New Zealand species if they were considered congeneric with the type species of *Donacilla* rather than with *Mesodesma* Deshayes, 1832, which would otherwise be available for them. Beu (1971a) has made an application to the International Commission on Zoological Nomenclature which, if accepted, will reduce *Amphidesma* to a synonym of *Semele* Schumacher, 1817, and replace *Amphidesma* in the family Mesodesmatidae with *Donacilla* de Blainville, 1819. Beu (1971b) considers that the genus *Donacilla* should not include the large New Zealand Mesodesmatidae and places them in the genus *Paphies* (Lesson, 1831). He has subdivided *Paphies* into four subgenera:

Subgenus *Amesodesma* Iredale, 1930; southern Australia.

Subgenus *Ceronia* Gray, 1853; eastern North America.

Subgenus *Mesodesma* Deshayes, 1832; New Zealand and South America.

Subgenus *Paphies*; New Zealand.

Beu (1971b) suggested the named New Zealand forms of *Paphies (Mesodesma)* as:

P. crassiformis (Marshall and Murdoch, 1920); Pleistocene.

P. subtriangulata subtriangulata (Wood, 1828); Pleistocene to Recent; Recent in northern New Zealand (tuatua).

P. subtriangulata quoyi (Deshayes, 1832); Pliocene to Recent; Recent in southern New Zealand (pipi).

P. subtriangulata porrecta (Marwick, 1928); Pleistocene to Recent; Recent in the Chatham Islands.

P. ventricosa (Gray, 1843); Pleistocene to Recent; Recent on mainland New Zealand (toheroa).

Paphies (Mesodesma) subtriangulata quoyi includes the *Amphidesma forsterianum* (Finlay, 1827) of earlier authors, and the term pipi is also used in the North Island for *Paphies australis australis* (Gmelin, 1791).

DISTRIBUTION

The toheroa, *P. ventricosa,* is restricted to the mainland of New Zealand and the present known distribution is shown (Fig. 2). It is most abundant on the long exposed ocean beaches of the west coast of the North Auckland Peninsula. These are Ninety Mile Beach, Dargaville beach, and Muriwai Beach. Other important populations are on the west coast of the Wellington district at Foxton, Waitarere, Hokio, Otaki, and Waikanae Beaches and in the extreme south of the South Island at Te Waewae and Oreti Beaches.

Minor sites on the North Auckland Peninsula are the west coast beaches of Mitimiti, Whangape, Piha, Pollok, and the east coast beaches of Tokerau and Te Arai. Toheroa have been recorded at Spirits Bay and Tom Bowling Bay, on the extreme northern coast. They have also been found in the North Island at Opotiki and Ohope Beaches, in the Bay of Plenty. Ohope Beach was a site of some minor importance before 1936 (see Hefford 1927–45, Cassie 1955). Street (1971) recorded a small bed on Hampden Beach and occasional specimens at Waikouaiti Beach and Long Beach, on the east coast of the South Island near Dunedin.

Some sand-scoured shells have recently been found on a beach 30 km north of Karamea on the north-west coast of the South Island, but living specimens have not been reported from this area (W. Simpson pers. comm.).

There is a popular belief that the North Island east coast populations have resulted from transplanting toheroa from the west coast, but this has yet to be confirmed.

EXPLOITATION

There is little record of the rate of Maori utilisation in pre-European times. There are, however, some data on the commercial fishery and the recreational fishery after 1900.

COMMERCIAL FISHERY

A cannery was opened on Dargaville beach in 1904, and by 1911 there were two canneries and the beach had been subdivided into four commercial concessions. There was also a small wet fish trade. By 1923 only one cannery remained on Dargaville beach, but a second was opened on Ninety Mile Beach. The Dargaville cannery operated for a short period in most years until recent times, but since 1967 harvesting has been intermittent. By 1945 the toheroa population on Ninety Mile Beach had fallen considerably, and the cannery was closed. It reopened for a short period from 1962 to 1964.

At various times and for very brief periods toheroa have been canned from Muriwai Beach, the Wellington district beaches, and Te Waewae Beach.

The commercial production reached a peak in 1940 with 77,000 kg of canned toheroa products, but since then production has exceeded 20,000 kg only nine times (Fig. 4). Until 1962 the production figures in the New Zealand Marine Department

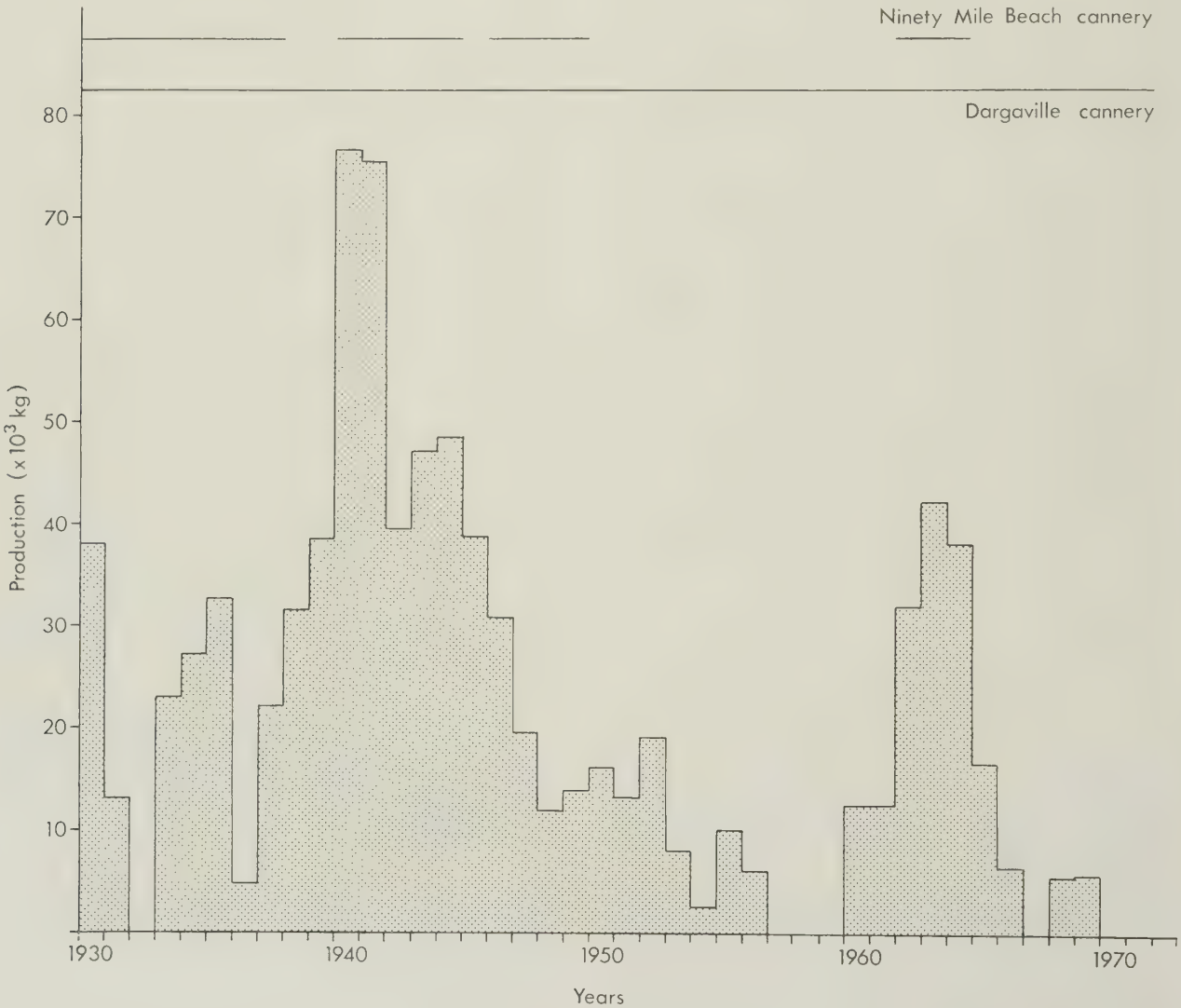


Fig. 4: Annual commercial production figures for the canneries operating off the North Auckland beaches, 1930 to 1970. The production figures are in kilograms of canned products. Toheroa are canned whole, minced, or as soup. The numbers of toheroa that these figures represent are not known.

records were quoted only as pounds weight of canned toheroa, and there is no definite conversion ratio to determine the numbers of animals involved. The Ninety Mile Beach cannery used to operate for 3 months a year, and toheroa were dug at a rate of about 9,600 per day for 5 days a week—an annual quota of some 576,000 toheroa. In 1962 the Marine Department began to issue quotas to the canneries based on the population estimates from the annual surveys. The annual take by the Dargaville cannery is shown (Table 1, estimates from records of Meredith Bros.).

RECREATIONAL OR AMATEUR FISHERY

The amateur fishery has generally increased with the rise in the number of motor vehicles. Hefford (1928) reported that the Muriwai Beach population was depleted in 1928 and that there were few toheroa adjacent to vehicular entrances to most beaches. By 1932 the following conservation regulations had to be introduced:

1. A 2-month closed season (October to November).
2. A quota system for Europeans (50 toheroa per person per day).
3. A minimum size limit of 3 in. (7.6 cm) shell length.

A personal quota of 80 toheroa per person per day was introduced for the Maori population in 1941.

Despite these regulations the rate of exploitation increased, and between 1932 and 1954 certain beaches had to be closed for various periods. By 1954 the beach population barely withstood the public harvest.

In 1955 the regulations were amended to reduce:

1. The personal quota of everyone to 20 per day.
2. The open season to 2 months a year, generally July and August.

Since 1962 the regulations have been amended according to the conditions at the time, and amendments have been based on the findings of the annual surveys. The major changes during this time have been to reduce the open season in the North Island to 14 days and to compel the public to dig toheroa by hand.

In 1967 all the North Island beaches were closed for that season; the Wellington west coast beaches have since been closed from 1970 and Ninety Mile Beach has been closed from 1971.

TABLE 1: Estimated exploitation rates on Dargaville beach, 1962-71

Year	Season (days)	Amateur fishery No. of vehicles	Amateur fishery Est. range of harvest (x 10^3)	Commercial fishery estimated harvest (x 10^3)	Estimated total population (x 10^3)
1962	62	—	—	541	20,500
1963	62	—	—	681	18,100
1964	62	—	—	752	12,800
1965	62	—	—	531	15,300
1966	62	8,000*	160-800*	159	13,200
1967	closed	—	—	—	4,200
1968	14	37,000	740-3,700	191	4,800
1969	14	21,889	438-2,200	185	7,300
1970	14	17,986	351-1,800	—	9,700
1971	10	20,000	400-2,000	—	3,200

* Estimate covers one weekend only of the season.

The public harvest values are estimates based on a minimum of 20 toheroa per vehicle if it had only one person in it and on a maximum of 100 toheroa if it had more than one person in it. It is unlikely that any vehicle would leave the beach with fewer than 20 toheroa. The figure is likely to be within this range.

The commercial harvest quantities are reasonable estimates based on Meredith Bros. and Company Ltd. data.

The population data are derived from Marine Department annual surveys.

Estimates of the public harvest have been made, but unless all vehicles leaving the beaches are stopped and examined, these estimates can be only guesses. Greenway (1963) estimated that over 1,000,000 toheroa were removed from Muriwai Beach during the 2-month season in 1963, and a similar number were estimated to have been taken from Dargaville beach during a weekend in the 2-month season of 1966, when 8,000 cars were recorded on the beach (J. K. Shea pers. comm.). There is some evidence that that season gave the largest harvest of toheroa, at least in recent years.

Since 1968 Hobson County Council has installed vehicle counters at the main road entrances to Dargaville beach during the open seasons, and the results are given (Table 1).

There is also an unknown degree of illegal taking of toheroa. Greenway (1972) considers that this may not be very significant, but in the author's experience one rarely visits a toheroa beach without seeing some evidence of poaching.

Between 1964 and 1971 the population of toheroa on Dargaville beach declined from about 10,000,000 to 1,000,000 (Greenway 1972).

ECOLOGICAL FEATURES OF DARGAVILLE BEACH

PHYSICAL FEATURES

General

Dargaville beach spans a distance of some 72 km from the north headland of Kaipara Harbour to the rocky outcrop of Maunganui Bluff. For much of this distance the coastline is almost straight and lies in a north-west plane (Fig. 3). North of Glinks Gully the littoral is backed by steep sandstone crags and hills, some 60 to 90 m high; to the south there is an intervening region of sand dunes.

The dune region varies in width and height from north to south. It is 90 m wide at Glinks Gully and 3 m at the southern end; the height ranges from 2 to 100 m in the same distance. The littoral also varies in width from north to south, being about 180 m wide at the north end of the beach and 300 m at the south end. Measured profiles over the mid-sections of the beach show an average inclination of 1 in 40 (Fig. 5).

In the sub-littoral the bottom shelves gradually, with an average inclination of 1 in 125 to a depth of about 4 m below chart datum, about 500 m off shore. The inclination steepens to 1 in 60 between 500 and 1,500 m to a depth of 20 m below chart datum. At about 3 km off shore the depth is 60 m.

Beach Material

Cotton (1951) showed that the west coast of the North Auckland Peninsula is composed of volcanic material largely derived from the central volcanic district of the North Island. This material is carried out to sea by the Waikato River and is then moved north-west by current and wave action.

The beach material is quartz or felspar in the form of fine sand and with very small proportions of medium and very fine sand. A typical sample had the following proportions:

Medium sand	(0.5 to 0.25 mm)	0.17%
Fine sand	(0.25 to 0.125 mm)	98.13%
Very fine sand	(0.125 to 0.0625 mm)	1.70%

In some local areas the proportion of medium sand is increased to 30%. There is very little vertical sorting of the beach material. Occasional layers of rotting organic material are found a few centimetres below the surface in areas of dense toheroa aggregation. North of Glinks Gully there are occasional rock or lignite outcrops.

The rates of aggradation or degradation may be extremely rapid. Local changes in level of ± 1 m have been recorded over the period of one tide (Fig. 5). There is a general tendency towards aggradation at least on the southern half of the beach. The marker posts set up by Meredith Bros. in 1962 were placed in the front line of dunes backing the littoral zone. During the last 10 years a new line of dunes has formed in front of the original dunes and in some places they are at least as high as the first line.

The sub-littoral substrate also consists largely of fine sand with occasional rocky outcrops and large pieces of lignite. The latter probably originated from the shore deposits. There is also a band of shell debris between the depths of 36 and 60 m lying parallel to the coastline.

Salinity

The annual range of the salinity of the in-shore surface water was from 34.8 to 35.8 ‰, with a mean of 35.2 ‰.

The interstitial beach water at low tide is often brackish. Several small lakes have been formed in the dune region, and the littoral is traversed by small streams. Analysis of the beach water collected from the mean tide level at low tide at various points

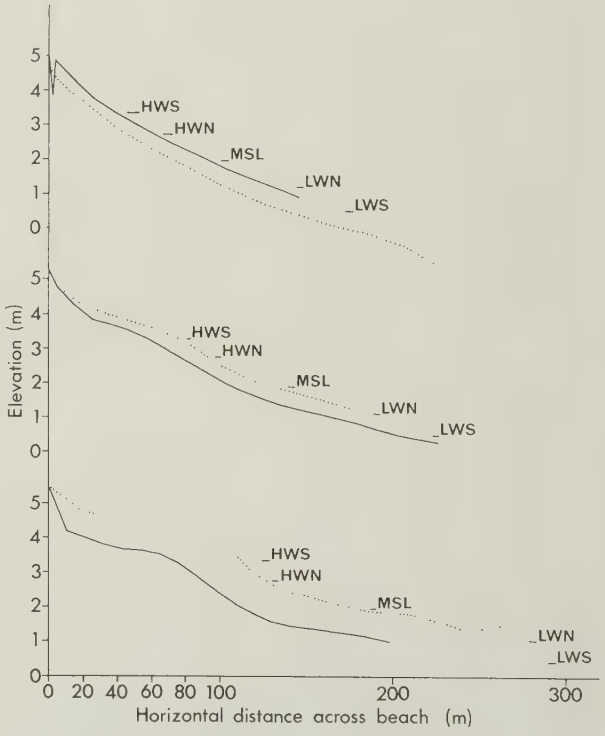


Fig. 5: Measured profiles across Dargaville beach at right angles to the wave front. The profiles were measured in February 1970 (solid line) and 14 days later (dotted line). The elevations of the sea level above chart datum are approximate (see page 11). The three positions are indicated by crosses in Fig. 3. HWS is high water springs, HWN high water neaps, MSL mean sea level, LWN low water neaps, LWS low water springs.

along the beach showed that the salinity may range from almost fresh water to completely saline. During 1969–70 water samples were collected from 16 stations (about 1.6 km apart) at monthly intervals to show the seasonal variation in freshwater seepage. However, the range of salinity from station to station was such that any seasonal variation was masked. The range of variation at one station was 3.7 to 35.38 ‰, with a mean of 20.10 ‰.

Rapson (1952) suggested a possible correlation between freshwater seepage and the presence of toheroa. This was not confirmed; toheroa aggregations have been found in areas in which the beach water was saline and in areas which were brackish.

Aggregations generally occur in areas where the water table lies close to the sand surface at low tide. Such areas are low lying and many are in the small bays along the beach which are the sites of small streams. Cassie (1955) records that the shell water of the toheroa is always saline.

Near-shore Water Circulation

Brodie (1960) indicated that the water circulation in the west coast region is influenced by two opposing currents. These are the West Auckland Current and the Westland Current. The West Auckland Current flows from the north and west of Cape Reinga down the Auckland west coast towards Kaipara Harbour. The Westland Current flows from the west of the South Island up to Cape Farewell and then less distinctly north along the Cape Egmont coastline and beyond towards Manukau Harbour.

However, Garner (1961) found the West Auckland Current to be highly variable and probably absent at times. When it does not flow, the Westland Current continues up the west coast of the North Island north of Cape Egmont. Stanton (1973) considers that the predominant summer coastal current in the Reef Point to Cape Reinga area (along Ninety Mile Beach) is north-westerly and the West Auckland Current when it exists flows south along the west coast towards Cape Egmont.

Wyrtki (1960) has produced monthly charts of the surface currents for the waters east of Australia between 5° and 48° S and 142° and 180° E from ships' observation data. In January and February the charts show that the north-easterly Tasman Current is divided in the coastal waters between Reef Point and Hokianga Harbour to form a north-flowing current along Ninety Mile Beach that sweeps round Cape Reinga and a south-flowing current along Dargaville and Muriwai Beaches. The March and April charts indicate north-flowing currents along the whole coast north of Cape Egmont. In May, June, and July the current diverges between Cape Reinga and Reef Point, and the northern component sweeps round Cape Reinga; the southern component flows down the west coast towards Cape Egmont. A north-flowing system persists along the whole coast in August, October, November, and December. In September the circulation diverges similarly to that shown in January and February.

There is thus great variation in the coastal water circulation along the west coast of the North Auckland Peninsula, and though the currents indicated were probably measured some distance off shore, they must have some profound effect on the near-shore circulation to produce a fluctuating north-south flowing system.

Empirical observation of the movement of plankton blooms close in shore suggests that the circulation pattern is similar to that described for La Jolla Beach by Shepard and Inman (1950). They found that the circulation was largely controlled by the wave convergence and divergence resulting from the diversified submarine relief outside the shore line. On Dargaville beach there is a consistent north-flowing along-shore current; drift material carried out to sea by the Wairoa River has been carried north at a rate of about 1.5 km per day. In shore of this current strong rip currents flow out from the shore at intervals, creating local along-shore currents with southerly and northerly components. Many of these rip currents are adjacent to the small bays in the littoral that are the sites of toheroa aggregation, and drift material is often concentrated in these areas.

Climate

The climate of northern New Zealand is only moderately diverse. The diurnal range of temperature at Dargaville is usually about 8°C, and the total temperature range usually lies between −2° and 30°C. The mean monthly air temperature ranges from 10° to 19°C, and the near-shore surface temperature of the sea ranges from 14° to 22°C.

The mean monthly climatological data for Dargaville are shown (Table 2). These data are derived from the published records of the New Zealand Meteorological Office. The results shown are the means of a 10-year period from 1961 to 1970. The sea temperatures are the means of 2 years' recording by the author during the experimental period.

The wind directions in Table 2 have been grouped according to the effect on the beach:

On shore—winds from the south, south-west, and west.

Off shore—winds from the north, north-east, and east.

Along shore—winds from the north-west and the south-east.

Calms.

TABLE 2: Climatological data (monthly means for the years 1961 to 1970)

Month	Temperature (°C) Air Mean	Air Abs. max.	Air Abs. min.	Sea Mean	Rainfall (mm) Mean	No. days	Sun (h) Mean	Wind direction (No. days) On shore	Off shore	Along shore	Calm
January	18.5	27.5	8.5	22	74	10	198	15	11	4	1
February	19.0	28.0	8.0	22	87	9	179	10	12	3	3
March	18.0	27.0	6.5	20	81	13	165	11	11	3	6
April	16.0	24.5	3.5	18	91	15	147	10	10	3	7
May	13.5	21.0	2.0	15	137	18	119	11	9	3	8
June	11.5	19.5	0.0	15	163	20	79	13	7	5	5
July	10.5	18.0	−1.5	14	121	20	102	12	10	4	5
August	11.0	18.0	−0.5	15	135	19	120	12	10	4	5
September	12.0	19.5	2.0	17	98	17	129	14	7	4	5
October	13.5	21.5	3.0	17	98	14	150	16	9	5	1
November	15.0	23.5	5.5	18	83	12	172	17	7	5	1
December	17.0	26.0	6.0	21	75	12	180	15	11	4	1
Year	14.6	28.0	−1.5	18	1,243	179	1,740	156	114	47	48

The data are derived from the New Zealand Meteorological Office monthly records for Dargaville, 1961 to 1970. The wind directions are explained in the text.

The temperature of the beach water at the mean tide level at low tide is generally within 1°C of the ambient sea temperature.

ASSOCIATED FAUNA

Littoral

The littoral fauna of Dargaville beach is similar to that of exposed sand beaches as described for northern New Zealand by Morton and Miller (1968).

Apart from the toheroa, four crustaceans (amphipods of the genus *Talorchestia* and isopods belonging to the genera *Scyphax, Pseudoaega,* and *Haustoria*) and representatives of four genera of polychaete worms, *Armandia, Glycera, Orbinia,* and *Aglaophamus,* were common on the beach, with two species of Nemertina. The polychaetes formed dense aggregations just below the mid-tide level. The vertical distribution and relative abundance of these species are shown (Fig. 6).

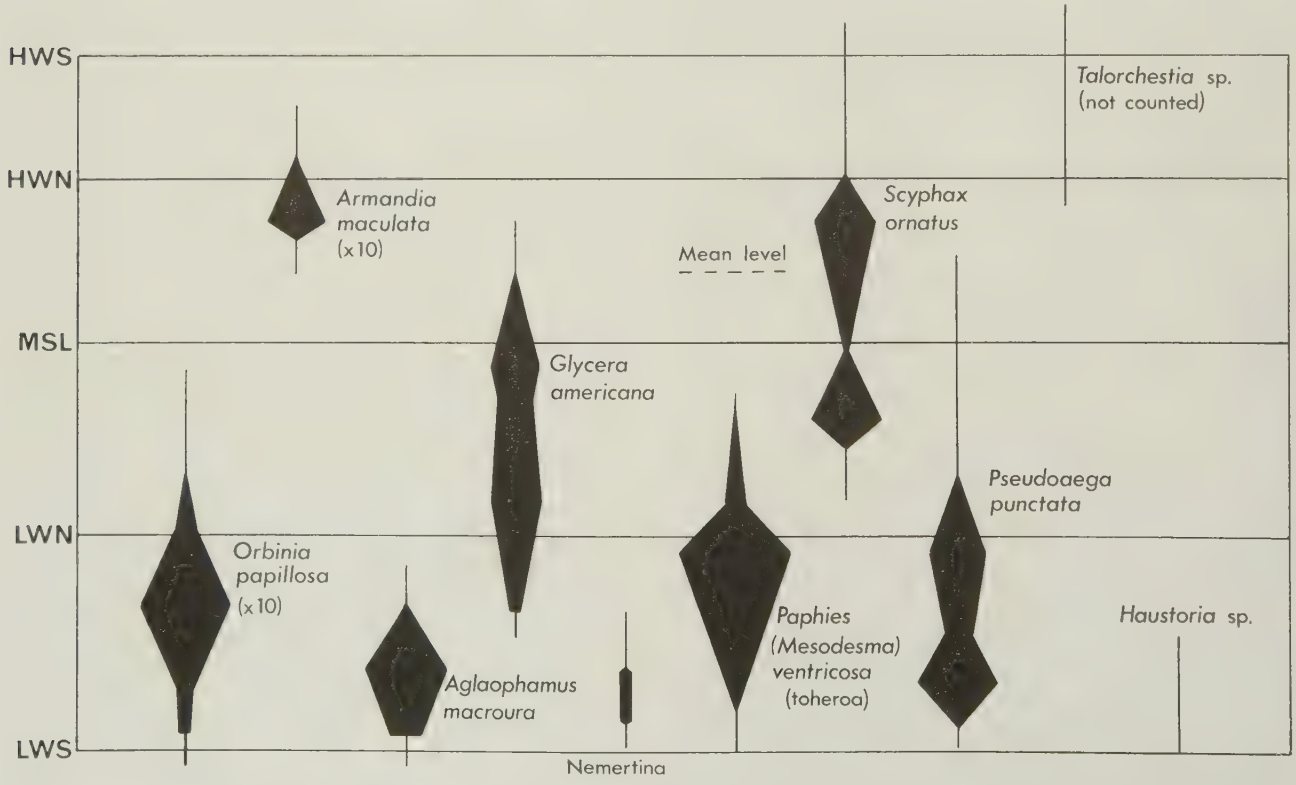


Fig. 6: Vertical distribution and relative abundance of the fauna on the littoral zone of Dargaville beach. The dotted line indicates the mean level of the toheroa population just before the sampling period.

The substantial increase in the area of beach occupied by polychaete worms and by the burrowing decapod *Callianassa filholi* Milne-Edwards on the Wellington district beaches after a severe decline in the toheroa population indicates that there is some degree of competition between these animals and the toheroa. Devine (1966) noted that the main food of *C. filholi* was *Chaetoceros armatum* T. West, which is also the toheroa's. The competition between the species may therefore be for food as well as space.

On most beaches the toheroa is the only permanent molluscan resident. Street (1971) has found occasional specimens of the bivalve *Macomona liliana* (Iredale) on the beach in Te Waewae Bay, South Island, and young stages of the tuatua, *Paphies (Mesodesma) subtriangulata subtriangulata,* are found on most North Island beaches. The littoral colonisation by the tuatua is generally only for short periods. Some, if not all, of the tuatua spat settle on the littoral each year and gradually move down shore as they grow until they eventually integrate with the adult population just below the level of low water springs.

On Dargaville beach such colonisation by the tuatua has usually been diffuse, but in November 1968 a dense aggregation of juvenile tuatua was found some 12 km south of Glinks Gully. In this aggregation a band (density 17.8 per square metre) extended for some miles along the beach between the levels of high water springs and high water neaps. Lower down the shore at the mid-tide level there was a more diffuse population of tuatua occupying the layer of sand above that occupied by the toheroa.

Tuatua appear to be important competitors for food and possibly also for space. Greenway (1969) reported that the toheroa population on a section of Ninety Mile Beach declined after a heavy spatfall of tuatua. Rapson (1954) suggested that there may be resurgent populations of toheroa and tuatua. The decline of toheroa populations on Ninety Mile Beach has been followed by an increase of the tuatua population in the littoral (Greenway 1969).

There is no evidence for tuatua-toheroa resurgence on Dargaville beach. As far as is known extensive aggregations of adult tuatua have never been found on the littoral (L. Game pers. comm.).

Sub-littoral

Samples of the sub-littoral fauna were collected with a modified Forster's anchor dredge 60 cm wide. This penetrated the substrate for some 7 to 15 cm when it was towed by the research vessel *Ikatere.* Samples were collected at 5-m depth intervals in the depth range 5 to 36 m from 9 stations along the beach. A few samples were also collected from a depth of 54 m.

TABLE 3: Species checklist: Sub-littoral fauna off Dargaville beach

Mollusca:	*Zeacumantus lutulentus* (Kiener, 1842)
	Maoricrypta monoxyla (Lesson, 1830)
	Struthiolaria papulosa (Martyn, 1784)
	Struthiolaria vermis (Martyn, 1784)
	Phalium (Xenophalium) pyrum pyrum (Lamarck, 1822)
	Buccinulum sp.
	Austrofusus glans (Roeding, 1791)
	Amalda (Baryspira) australis australis (Sowerby, 1830)
	Perna canaliculus (Gmelin, 1791)
	Myodora striata (Quoy and Gaimard, 1835)
	Dosinia anus (Philippi, 1848)
	Bassina yatei (Gray, 1835)
	Notopaphia elegans (Deshayes, 1854)
	Angulus gaimardi (Iredale, 1915)
	Gari lineolata (Gray, 1835)
	Mactra discors (Gray, 1837)
	Spisula aequilateralis (Deshayes, 1854)
	Paphies (Mesodesma) subtriangulata subtriangulata (Wood, 1828)
	Anchomasa similis (Gray, 1835)
	Octopus maorum Hutton, 1888
Echinodermata:	*Fellaster* sp.
	Astropecten sp.
	Ophionereis sp.
	Caudina sp.
	Cucumaria sp.
Crustacea:	*Ovalipes catharus* (White, 1843)
	Pagurus novaezealandiae (Dana, 1852)
	Balanus decorus Darwin, 1854
	Idotea sp.
Sipunculida:	*Dendrostoma* sp.
Polychaeta:	*Glycera* sp.
	Nereis sp.
Nemertina:	Two species

A checklist of the fauna collected is given (Table 3). Many empty mollusc shells were also brought up in the dredge, but these were not identified.

From the level of low water springs to about 100 m off shore (approximate depth 1 m) the tuatua and the swimming crab, *Ovalipes catharus,* were the dominant animals. From this point to about 600 m off shore (approximate depth 5 m) an echinoid, *Fellaster* sp., and the bivalves *Spisula aequilateralis* and *Dosinia anus* with the tuatua were the most numerous animals. Most of the species collected during the survey were found in this region. The remaining species in the checklist were common to most samples from depths down to 22 m, except for the bivalves *Bassina yatei* and *Angulus gaimardi* and the echinoid *Fellaster* sp., which were restricted to depths shallower than 16 m.

Several of the molluscs were common in many samples: *Struthiolaria papulosa, Austrofusus glans, Amalda (Baryspira) australis australis, Mactra*

discors, *Myodora striata*, and *Spisula aequilateralis*. The bivalves were also found in fairly dense aggregations.

Some of the species listed in Table 3 were collected from a block of lignite dredged up from 36 m. These were the molluscs *Zeacumantus lutulentus*, *Buccinulum* sp., *Anchomasa similis*, *Notopaphia elegans*, and *Perna canaliculus*. A crustacean belonging to the genus *Idotea*, a sipunculid of the genus *Dendrostoma*, and a polychaete of the genus *Nereis* were also collected from this habitat. *Perna canaliculus* was also collected with some algae from a rocky outcrop in 16 m of water at the northern end of the beach.

Off-shore dredging was also carried out to establish whether there was a sub-littoral population of toheroa as suggested by Cassie (1955) and Waugh and Greenway (1967). The result of this investigation was negative. The dredge digs into the substrate only to a maximum depth of 15 cm, whereas toheroa on the beach have been known to dig deeper than 20 cm. During the present investigation a few fragments of toheroa shell were collected. These were from very large shells over 15 cm long and similar to those occasionally cast up on the beach and recorded by Cassie (1955).

CONDITION AND REPRODUCTION

CONDITION

Two previous authors have indicated the general pattern of the change in condition with time.

Rapson (1952) compared the wet weights of the edible meat and the whole animal (shell plus meat). These data were derived mainly to estimate the quantity of meat available to the cannery, but they also showed factors pertaining to the quality of the animals. From December to May the condition was below average and from June to November it was above average. The ratio of edible meat to total weight was higher in small toheroa (28%) than it was in large toheroa (22%), and it also varied less for toheroa under 7.5 cm than it did for toheroa over 7.5 cm.

Cassie (1955) used data derived from the cannery production figures. Condition was expressed as a ratio of the number of bushels of whole toheroa needed to produce 1 bushel of meat. The condition improved from June to August, 6:1 to 5:1 or 4:1, and began to decline towards the end of September, reaching a low of 7:1 or 8:1.

During the present study the condition was measured at about monthly intervals from November 1968 to January 1971 with the technique described by Baird (1958). In this technique the condition is expressed as the percentage of the volume of the shell cavity occupied by meat (edible meat plus the mantle, etc.). The volumes of the whole animal, the shell, and the meat are measured while they are still wet. The shell cavity is the total volume minus the shell volume.

Owing to their size it was feasible to measure the condition of individual toheroa. Sample numbers ranged from 26 to 85, and the standard deviations of the means ranged from 4 to 12, with a mean of 7.

The correlation between size and condition noted by Rapson (1952) was found to be linear for some samples. For example, the correlation coefficient for one sample of 65 individuals was 0.577, significant at a probability level of $P = 0.05$. The total volumes in this sample ranged from 8 to 158 ml, and the condition ranged from 38 to 80%. Total volume was used as a measure of size, as it expresses all combinations of length, width, and depth.

Since the correlation between size and condition was not always significant, the smaller toheroa may have had a different gonadal cycle from that of the larger toheroa. Samples were subdivided into two length groups: those greater than 9.0 cm and those smaller than 9.0 cm. This size division was based on the fact that the curve relating total volume to shell length shows an increased inflection at about 9.0 cm (Fig. 7). After 9.0 cm the relationship becomes almost linear up to 13 cm.

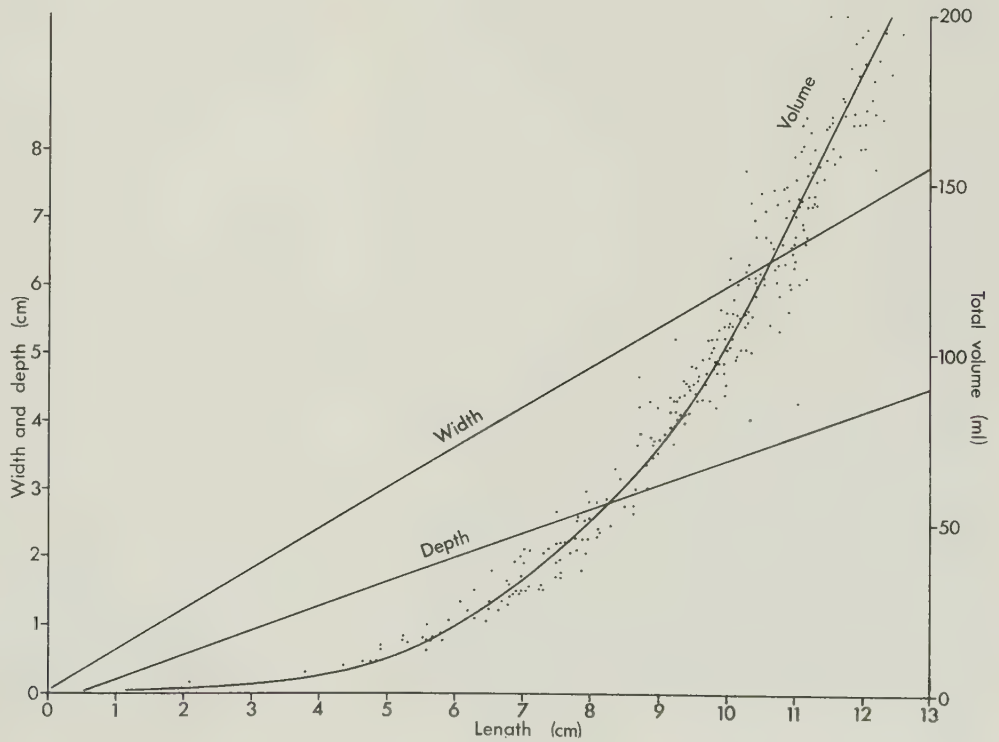


Fig. 7: Shell length-width, length-depth, and length-total volume relationships for the toheroa.

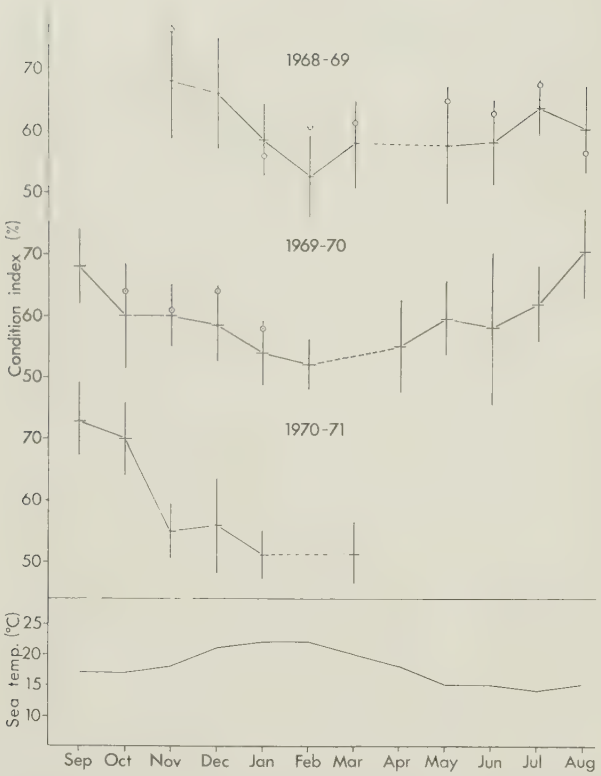


Fig. 8: Variation in the condition of toheroa with time. Samples of toheroa under 9.0 cm shell length and over 9.0 cm (joined points) were measured. The mean values are plotted with the standard deviations for the samples over 9.0 cm. The mean monthly sea temperatures are also indicated.

The mean condition for the two groups is plotted against time (Fig. 8). The standard deviations of the group greater than 9.0 cm are indicated. Those for the group less than 9.0 cm are similar. Though the condition of small toheroa is generally higher than that of large toheroa, the pattern of condition change with time is similar. Small toheroa lose and gain condition faster than large toheroa, but the cycle of gonadal change appears to be similar.

The condition generally reaches a maximum in August or September, coincidental with rising temperatures. It then drops to a minimal value in January or February, which corresponds to the first major flush of spawning. There is then a slight increase in the condition in March or April, followed by a period of fluctuation in May-June, July, or August, which corresponds to the secondary spawning periods (see page 25). These latter periods of spawning occur when temperatures are falling. There is then a rapid increase in condition to the August-September peak.

Differences in condition between toheroa of similar size from isolated or aggregated populations are not significant; nor is there any significant change in the condition from north to south along the beach.

REPRODUCTION

There are no external sexual characteristics, though occasionally female toheroa can be distinguished by the granular appearance of the gonad when it is incised. Accurate sexual differentiation is possible only through the examination of smear preparations or stained sections.

Individuals from all size groups were sampled for histological examination at about monthly intervals. Sample numbers ranged from 30 to 80. Pieces of tissue were excised from the central region of the gonad posterior to the digestive diverticula and were preserved in sea water Bouin's fluid. Small specimens were preserved whole. Blocks of tissue were cut from the centre of the sample to eliminate distortion due to the fixative. Sections were cut at 4 to 7 μm and were stained with haematoxylin and eosin.

All the toheroa examined were unisexual; of 1,037 toheroa 501 were male and 536 female. Dawson (1954) found a few hermaphrodites in *Paphies (Mesodesma) subtriangulata quoyi,* but in most the sexes were separate and in equal proportions.

Development of the Gonad

Dawson (1954) found that *P. subtriangulata quoyi* became sexually mature within 3 years and that some animals had active gonads in the second year. Rapson (1952) found that few toheroa under 3.8 cm (10 to 12 months old) were sexually mature and that most toheroa became mature in their second year. The present study confirms these data.

In 1-month-old spat with a mean length of 7 mm the undifferentiated gonad forms a mass of connective tissue and primary germ cells lying round the style sac. The primary germ cells have very little protoplasm and rounded nuclei. Follicles form shortly after this stage and the lumina are often filled with reticulate cells. Lobes of the gonad extend up into the digestive diverticula and down into the foot.

Three months after spatfall about 20% of the juveniles had fully developed gonads, the females having follicles with ovocytes and free ova and the males having follicles with spermatocytes, spermatids, and spermatozoa. The mean shell length at this age was 1.0 cm, but sexually developed individuals tended to be larger, often nearer to 1.5 cm. Nine months after spatfall (mean length 3.15 cm) some 75% were sexually mature and by 15 months (mean length 4.7 cm) all were mature.

Phases of Gonadal Cycle

Five phases similar to those described by Ropes (1968) for *Spisula solidissima* Dillwyn could be distinguished in the gonadal cycle. These were never well defined and in most samples there was a fine

gradation from one phase to the next. In this bulletin the partially spawned and spent phases of Ropes (1968) have been combined, as only isolated examples of the latter were found under natural conditions.

The phases of the toheroa gonadal cycle are:

Female Gonads

1. Early active phase (Fig. 9A). The follicle walls are not completely contracted and most follicles have lumina. Some free ova and late active ovocytes persist from the last ripe phase. There is much ovogenetic activity, and the follicle walls have a thick appearance because of the many primary germ cells. Many early ovocytes are attached to the follicle walls by broad cytoplasmic bases. The ovocytes are usually hemispherical or cylindrical with rounded apices. The nucleus occupies most of the cell volume. The follicle size ranges from 0.30 to 1.67 mm in circumference, with a mean of 0.66 mm.

2. Late active phase (Fig. 9B). Free ova and ovocytes are much more numerous than in the early active phase, and the follicle walls are less dense. More mature ovocytes are larger and are irregularly cylindrical or ovate, and the nuclei occupy less of the total cell volume. The basal attachment to the follicle wall is narrow and in ovocytes that are almost ripe the basal attachment is a narrow stalk. The mean size of the follicle tends to be slightly larger, but the range of size is similar: 0.38 to 1.56 mm in circumference, mean 0.84 mm.

3. Ripe phase (Fig. 9C). In ripe gonads there are many irregularly shaped oval to round free ova almost filling the lumina of most follicles. The

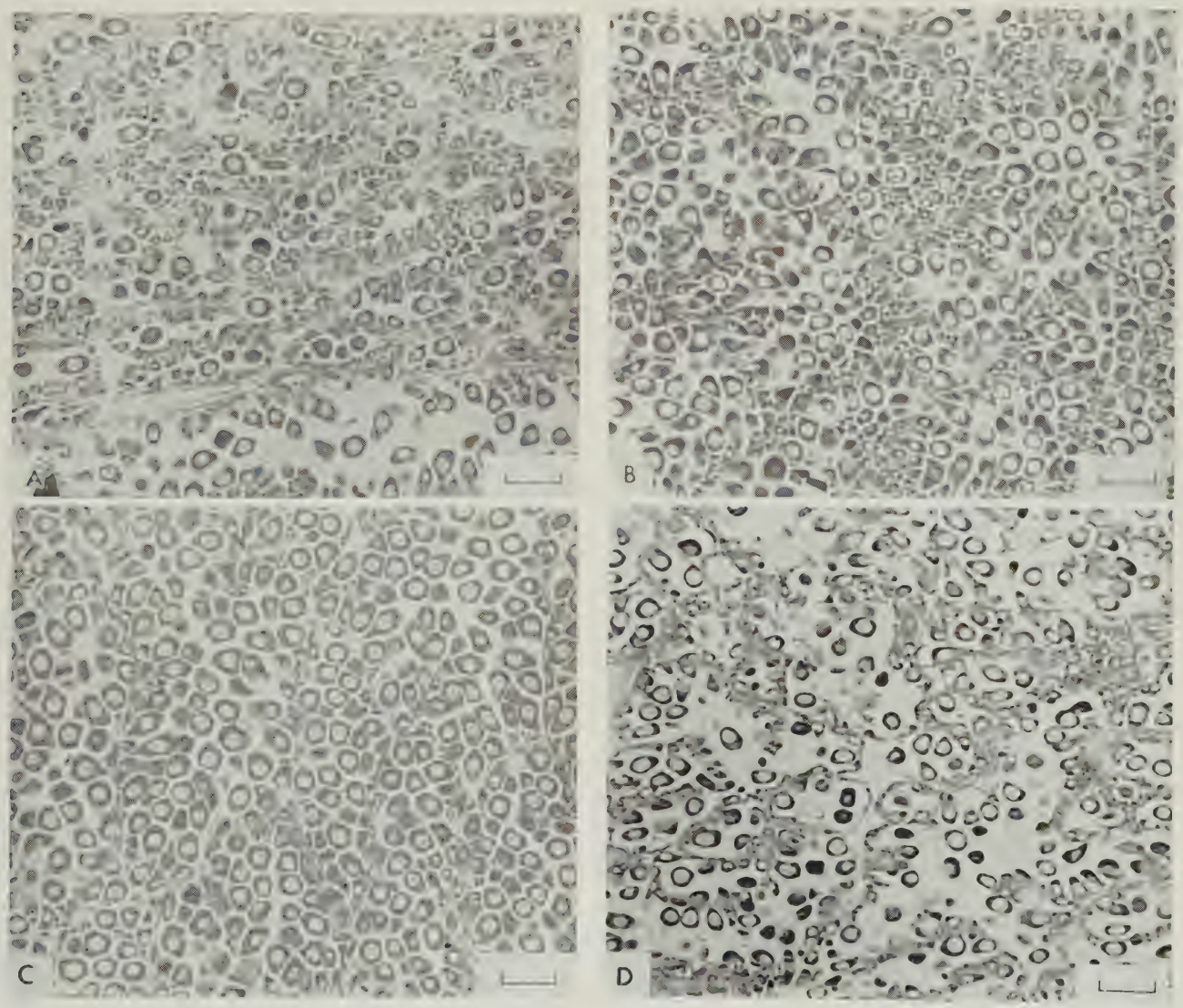


Fig. 9: Sections of gonadal material from a female toheroa: A—early active phase. B—late active phase. C—ripe phase. D—partially spawned or spent phase. Scale 100 μm.

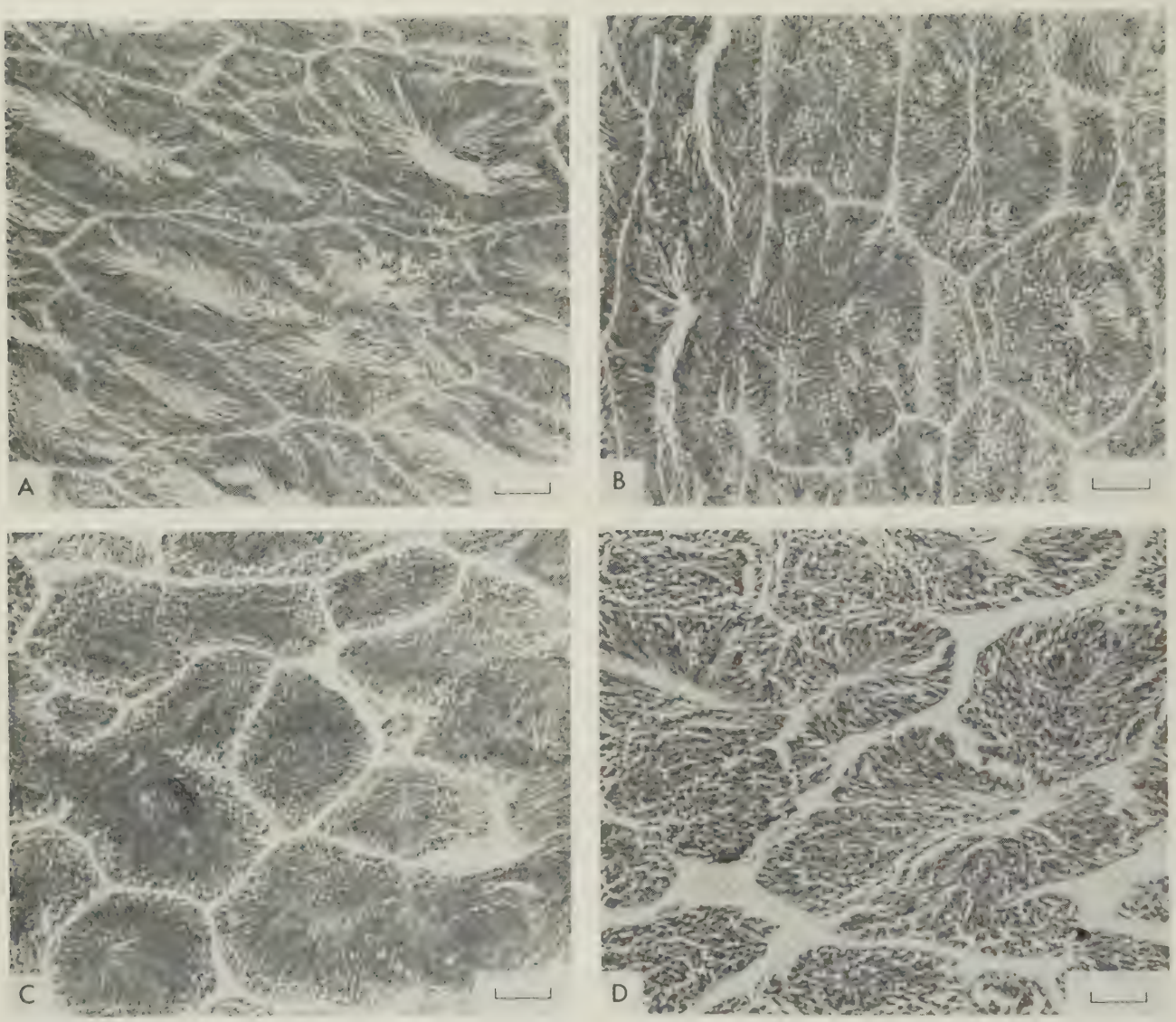


Fig. 10: Sections of gonadal material from a male toheroa: A—early active phase. B—late active phase. C—ripe phase. D—partially spawned to spent phase. Scale 100 μm.

follicle walls are thin, consisting of a few strands of connective tissue and a few primary germ cells. Ovocytes are few and most are in the early active phase. A very few almost ripe ovocytes persist with very narrow basal stalks. The follicle size ranges from 0.35 to 2.09 mm in circumference, with a mean of 0.99 mm.

4. Partially spawned to spent phase (Fig. 9D). The follicle walls are contracted and still thin in the partially spawned phase. Some follicles are partially ruptured. A few free ova are present in the lumina, and some ovocytes are attached to the follicle walls. There was no evidence of large-scale resorption of ova.

In the spent condition there are generally no free ova. The follicle walls are contracted and are thickened with connective tissue and primary germ cells. A few early ovocytes are attached to the follicle walls.

The follicle size in partially spawned to spent toheroa ranges from 0.17 to 1.67 mm in circumference, with a mean of 0.56 mm.

Male Gonads

1. Early active phase (Fig. 10A). The follicle walls are thin and have a layer of spermatogonia. Spermatocytes and spermatids proliferate throughout the lumina in about equal proportions. In some their distribution is radial, rows of spermatocytes followed by spermatids radiating towards the centres of the lumina. In others the distribution is more random, with blocks of spermatocytes interspaced with blocks

of spermatids. At the centres of many lumina there are a few spermatozoa.

2. Late active phase (Fig. 10B). A layer of spermatogonia lines the follicle walls and the spermatocytes and spermatids occupy about one-third of the lumen space. In some follicles there are more spermatocytes than spermatids. Some of the latter radiate in towards the centres of the lumina. The centres of most lumina are loosely packed with radiating bands of spermatozoa.

3. Ripe phase (Fig. 10C). In the ripe phase a dense mass of spermatozoa fills most of the lumen space. In some lumina the spermatozoa swirl towards the centres; in others the distribution is more homogeneous. A thin layer of spermatocytes and spermatids occupies the remainder of the lumen space.

4. Partially spawned to spent phase (Fig. 10D). In the partially spawned phase loosely packed groups of spermatozoa still occupy the centres of the lumina. The follicle walls are slightly contracted and there are few spermatogonia. The spermatocytes and spermatids generally form a narrow band round the lumen periphery.

In spent toheroa there are few if any spermatozoa, and the follicle walls are contracted, which crowds the spermatocytes and spermatids. The follicle walls are dense and the spaces between follicles are sometimes packed with undifferentiated cells.

Annual Cycle

No long resting or inactive phase was apparent under natural conditions. Free ova or spermatozoa were present in mature toheroa gonads throughout the year.

Varying proportions of the populations were more or less ripe during the whole year (Fig. 11). However, there was a tendency for increasing proportions to ripen during periods when the sea temperatures were rising. From July to October the sea temperature increased from 14° to 17°C, and by September or October about 60 to 80% of the population were ripe. The rest of the population ripened shortly after, in the period October to November.

Partial spawning occurred shortly after the clams were ripe, and the gonads were quickly recycled through the early and late active phases to a second ripe phase in December to January, when the sea

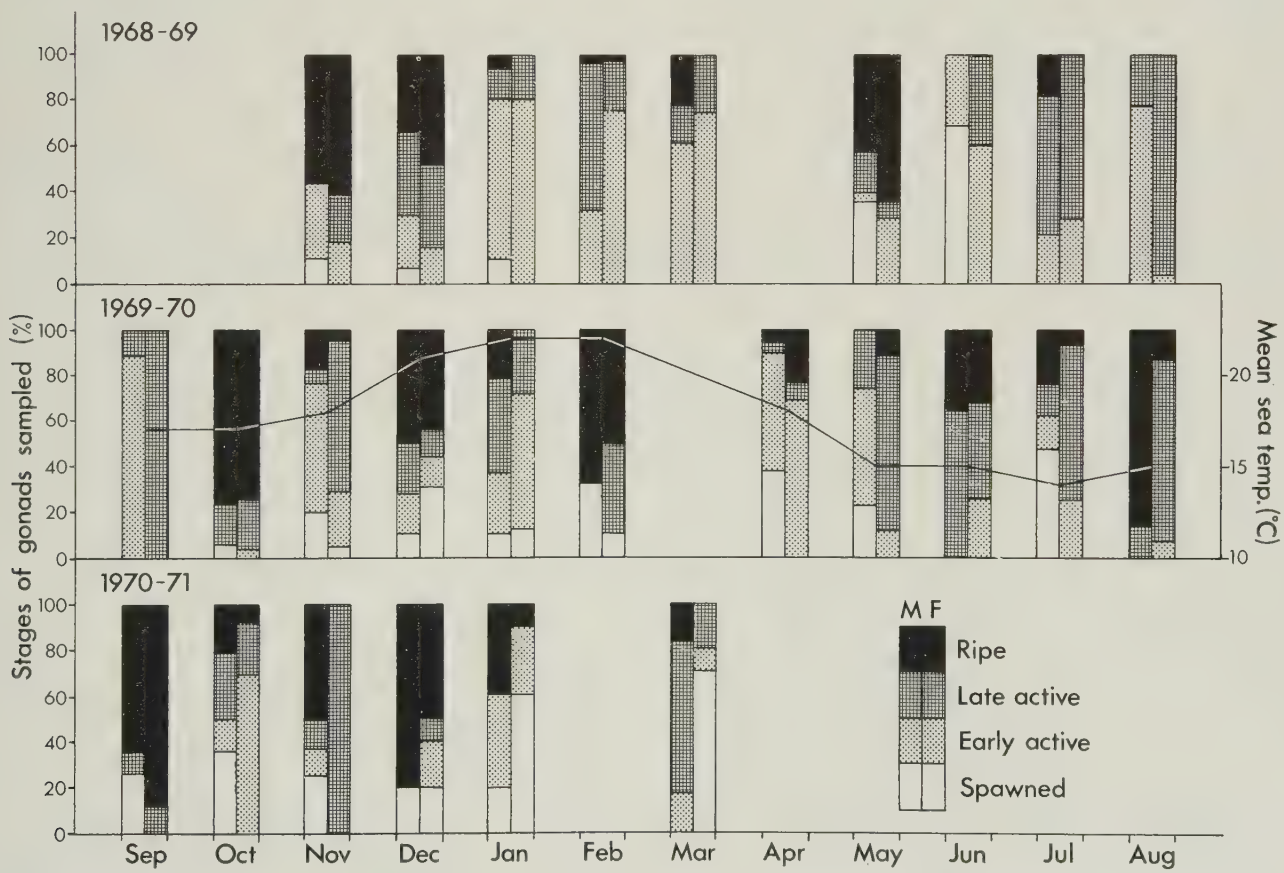


Fig. 11: Annual gonadal cycle of toheroa on Dargaville beach from November 1968 to March 1971. The mean monthly sea temperatures are also indicated.

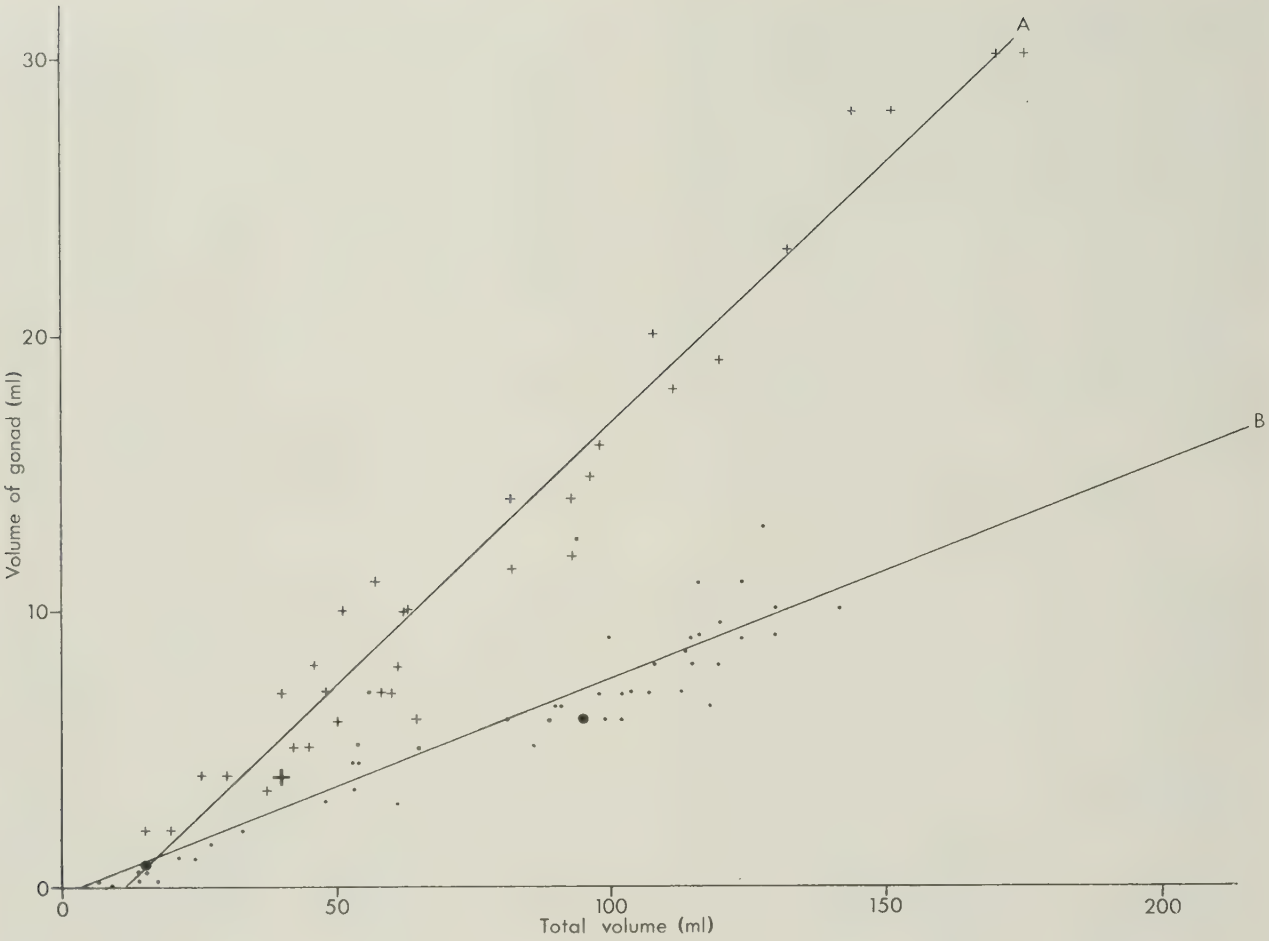


Fig. 12: The relationship between volume of gonad and the total volume of ripe toheroa (A), sampled in September, and toheroa after the first annual spawning period (B), sampled in January. The larger symbols indicate where two points coincide.

temperature had increased to 22°C. In some years there is a third period in February when some 50% of the population have ripe gonads. From February to June, when the sea temperatures were decreasing, small proportions of the population had ripe gonads. In July or August most toheroa were in the early to late active phase ready to start the next year's cycle.

From September to January the condition of the toheroa dropped from a maximum (mean in excess of 70%) to a minimum (mean in excess of 50%), and the gonadal volume decreased (Fig. 12). During the primary ripe phase in September or October the gonads were distended and packed with ripe ova or spermatozoa, but during subsequent ripe phases they were more flaccid, and the numbers of free ova or spermatozoa decreased per unit area of histological section. The numbers of available ova or spermatozoa may hence be considerably reduced after the initial peak, and the first spawning period from September to February appears to be the major reproductive period during the annual cycle.

Significant spatfalls have also been recorded in May, June, and July, which may have been due to a greater proportion of the population being ripe at this time than normal or to the environmental conditions being favourable to spatfall.

FECUNDITY

It is difficult to make reasonable estimates of the fecundity of an animal capable of spawning at any period during the annual cycle. Dawson (1954) measured the volume of ova stripped from ripe tuatua and toheroa and estimated the numbers to be about 30,000,000 to 40,000,000 and 80,000,000 to 90,000,000 respectively. This, however, assumed only one period of spawning a year. Davis and Chanley (1955) conditioned and spawned the oyster *Crassostrea virginica* Sacco and the clam *Venus*

mercenaria Linnaeus to establish levels of fecundity. This treatment had to be continued for 2 to 3 months until the animals were spent. Their results for the clam *Venus mercenaria* ranged from 8,000,000 to 39,500,000 ova, with a mean of 24,600,000. They also established that there was some correlation between the size of the animal and the number of eggs produced: ". . . about 15% of the variation in total egg production could be attributed to the differences in size of the female clams used in the experiment". So far attempts to induce spawning in the toheroa have been only moderately successful and inadequate for fecundity estimates.

There is a linear relationship between the volume of the gonad and the volume of the whole animal. Measurements were taken on animals with a high mean condition (mean 73%) in September 1970 and with a low mean condition (mean 56%) in December 1970. At both times most animals were in the ripe phase of the reproductive cycle, but there had been a period of spawning between the two samples (Fig. 12).

As the gonad and the rest of the tissues lie very near to one another, it is difficult to excise the complete organ. A standard region of the body was therefore chosen in which most of the tissue was gonadal material. It was assumed that the volume of the remnants of other tissue excised with the gonad would cancel out the volume of the remnants of gonadal tissue not excised.

The September sample consisted of 35 animals ranging in total volume from 15 to 175 ml and in gonadal volume from 2 to 30 ml. The correlation coefficient was 0.98, significant at $P = 0.05$. Similarly the January sample consisted of 51 animals ranging in total volume from 6 to 142 ml and in gonadal volume from 0 to 12.5 ml. The correlation coefficient was 0.91, significant at $P = 0.05$ (Fig. 12). The number of eggs liberated during spawning is likely to be related to the loss in volume of the gonad and to the condition.

Examination of the gonadal cycle data (Fig. 11) indicates that the average number of spawnings of a toheroa per year is 2.5. The mean number of free ova per unit area (0.4 sq mm of a histological section) for ripe gonads is 44 and the mean diameter of an egg is 0.05 mm. By interpolation the estimated number of available eggs in a ripe gonad is about 2,000,000 per cubic centimetre or 5,000,000 ova per cubic centimetre per year.

The level of fecundity of a fourth-year animal is likely to be more than twice that of the combined second- and third-year animals provided that the latter have a similar spawning cycle.

LARVAL DEVELOPMENT, SETTLEMENT, AND SURVIVAL

LARVAL DEVELOPMENT

Attempts to rear larvae in the laboratory were not successful, though spawning was accomplished on two occasions by raising the temperature from 18 to 24°C and the larvae were kept alive for 4 days. Cleavage began some 2 h after fertilisation, and the straight-hinge veliger developed within 30 to 40 h (Fig. 13, upper). The mean length of the veliger was 90 μm. Later stages of larvae presumed to be those of the toheroa were isolated from plankton samples collected by manually towing a small conical net through the surf. In these stages the umbo had developed, and the larvae were more or less similar in shape to that of the smallest settled individuals collected from the beach (Fig. 13, lower). The length of the

Fig. 13: Larval stages of toheroa: Upper—straight-hinge veliger. Scale 0.1 mm. Lower—post-metamorphosis setting stage. The length of shell is 2 mm.

planktonic forms ranged from 200 μm to over 1 mm, and the smallest settled animal collected was 2 mm long.

Rapson (1952) estimated a planktonic life of 10 to 12 days for toheroa larvae, but there was an interval of at least 1 month between the first signs of spawning and the subsequent collection of spat from the beach. However, settled individuals less than 2 mm could easily have been missed.

SETTLEMENT AND SURVIVAL

Setting Period

Settled individuals of 2 mm were collected in the wave front and were carried up the beach by the surf at all stages of the tide. They settled during the interval of slack water just before each wave receded and quickly dug into the sand to a depth of 1 or 2 cm. Samples of these juveniles were collected by gently scraping the sand away or by scraping the sand to form a small pool of water and sand, which, because of the thixotropic effect, could be stirred and the spat floated out.

Settlement at any level on the beach was completely random and depended on the fetch of the particular wave that carried the spat ashore. On several occasions concentrations were found scattered along the strand lines of several successive waves. Initially the spat seemed to be unable to retain a good purchase in the substrate and were frequently washed out again by the surf. Their ability to maintain their position must depend on the degree of disturbance of the substrate. King (1959) indicated that the depth of disturbance on a sand beach was a function of the wave height at the break point and the wave energy. For an increase in wave height of 30 cm the depth of disturbance increases by 1 cm. As the west coast beaches are frequently pounded by heavy surf, the opportunities for stable colonisation must therefore be limited.

For some weeks after metamorphosis the juveniles must be continually settled, washed out, and redeposited by succeeding waves. This process gradually moves the juveniles up shore until they form a band just below the level of the high water mark. At this level the sand is generally damp during the period of low water. As they grow they gradually move down the shore, where they are able to maintain their position, despite the increased pounding by the surf, by burrowing deeper.

On several occasions juveniles were stranded in the dry sand above the high water mark by waves of greater than normal amplitude and their chances of survival appeared limited. The black-backed gull, *Larus dominicanus* Lichtenstein, and the red-billed gull, *Larus novaehollandiae scopulinus* Forster, prey on the juveniles during the setting and post-setting period. Black-backed gulls have also been observed to excavate larger individuals from the beach (P. Brunton pers. comm.).

During the study period spawning began in November 1968 and continued in the first instance until December 1968 or January 1969 (Fig. 11). Small numbers of spat were first found in early January 1969, but the lengths (3.2 to 13.3 mm) indicated that setting had begun earlier. By February 1969 the population had increased, and the size-frequency distribution indicated that the major set had occurred in January (Fig. 14). By March 1969 most of the spat from the first period of spawning had settled. There was a further minor period of spawning in May to June, and a small spatfall was recorded on the beach in August 1969.

In the following season, 1969–70, toheroa began to spawn in October 1969 and continued until February or March 1970. Spat were first recorded on the beach in mid December 1969, and setting probably began in late November or early December 1969. The frequency distribution of the shell length for the first-year group in May 1970 showed two peaks, which indicated a more discontinuous period of setting than in the previous season. Further periods of spawning occurred in June, July, and August, and a few juveniles were recorded as settling then.

During the 1970–71 season spawning began in September 1970 and continued intermittently until it was interrupted by the general mortality of toheroa which occurred in January and February 1971. This severely depleted the population and is discussed later.

Post-setting Period

It is considered that the 1968–69 spatfall was more successful than either the 1969–70 or the 1970–71 spatfall.

By June 1969, about 5 months after the spatfall had started, the juvenile band lying between the levels of high water springs and high water neaps was almost continuous over many kilometres of the beach. The band width over a 30-km section of the beach ranged from 0 to 15 m, with a mean of 5.4 m. The population density ranged from 0 to 48 per square metre, with a mean of 17 per square metre, and the estimated population was 2,750,000 over the 30 km of the beach.

The high density settlement areas are usually in the small bays along the beach, which are often the sites of adult toheroa aggregation. The rip currents adjacent to these small bays probably concentrate the spat just as they concentrate flotsam.

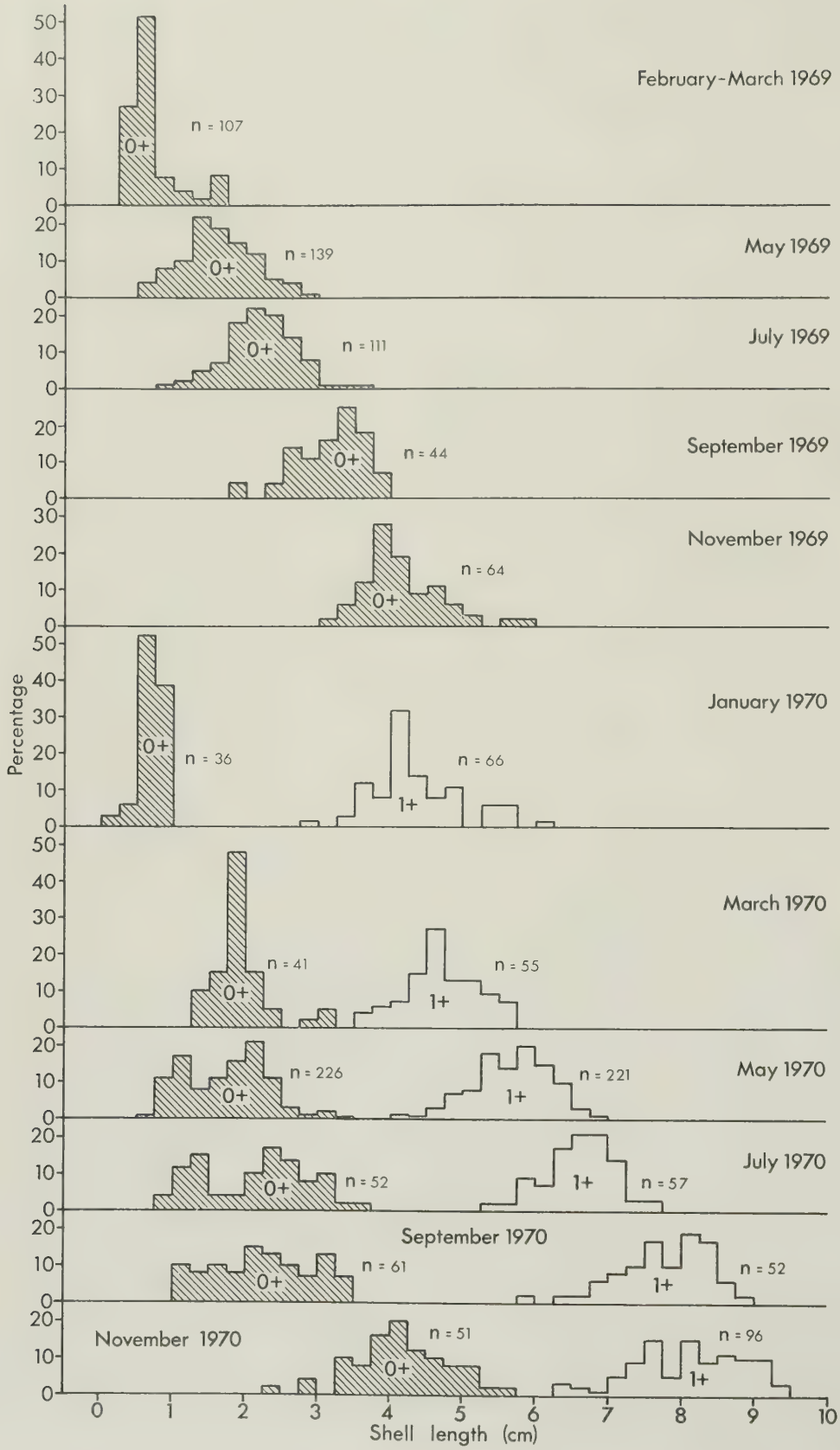


Fig. 14: Shell length-frequency distributions of juvenile toheroa from the 1968–69 and 1969–70 setting periods. Distributions are indicated at 2-monthly intervals in size groups of 2.5 mm.

During the following season (1969–70) the spatfall was more intermittent and though the juveniles were sorted towards the upper levels of the beach by the surf, the distribution was never as well defined as in 1969. Isolated spat, density about 1 per square metre, were found in situations outside the small bays along the beach, but in the bays densities ranged from 1 to 5 per square metre, and in June 1970 band widths were from 10 to 36 m.

In December 1970 a good settlement was recorded on the beach south of Glinks Gully. However, mortality in early 1971 heavily reduced the population. The juveniles were then still being sorted by the surf, and the band width ranged from 0 to over 45 m along 20 km of the beach. The density ranged from 0 to 14 per square metre, with a mean of 5.5 per square metre.

From July to September the juveniles began to move down shore, and by November most had colonised the mean tide level. The horizontal distance between the level of high water springs and the mean tide is on average 60 m, with a vertical drop of 1.5 m. The juveniles moved down shore about 15 m per month. During this time there was some degree of sorting with respect to size, and the larger animals tended to occupy the lower levels of the band.

There was also some lateral sorting, and when the mid-tide level was reached the juveniles had aggregated into beds. In some areas these coincided with established adult beds, but in others new, almost mono-age-group beds were found. These were usually small, many being less than 30 m long, but the juveniles were densely packed (in many beds over 100 per square metre). The juvenile beds that formed in the areas where an adult bed was already established occupied the layer of sand above that of the adults. Movement of the juveniles or the adults in these two layer beds indicated that the populations were not fully integrated. When such movement occurred the juveniles tended to move up shore from the mean tide level, whereas the adults tended to move down shore. Total integration of the layers did not appear to occur until some 18 months after spatfall.

During the second year many of the toheroa in the mono-age-group beds began to disperse and some disappeared entirely. In these examples some lateral movement appears to have occurred, as adult beds in adjacent areas showed a corresponding increase in their juvenile population in the same period.

Whole beds were moved during January 1969. The upper level of a bed (8 km south of Glinks Gully) the position of which had been fixed the previous evening was moved down shore for a horizontal distance of 30 m during the night. At this time the sea was moderately calm with only a small surf, and the tides were changing from springs to neaps.

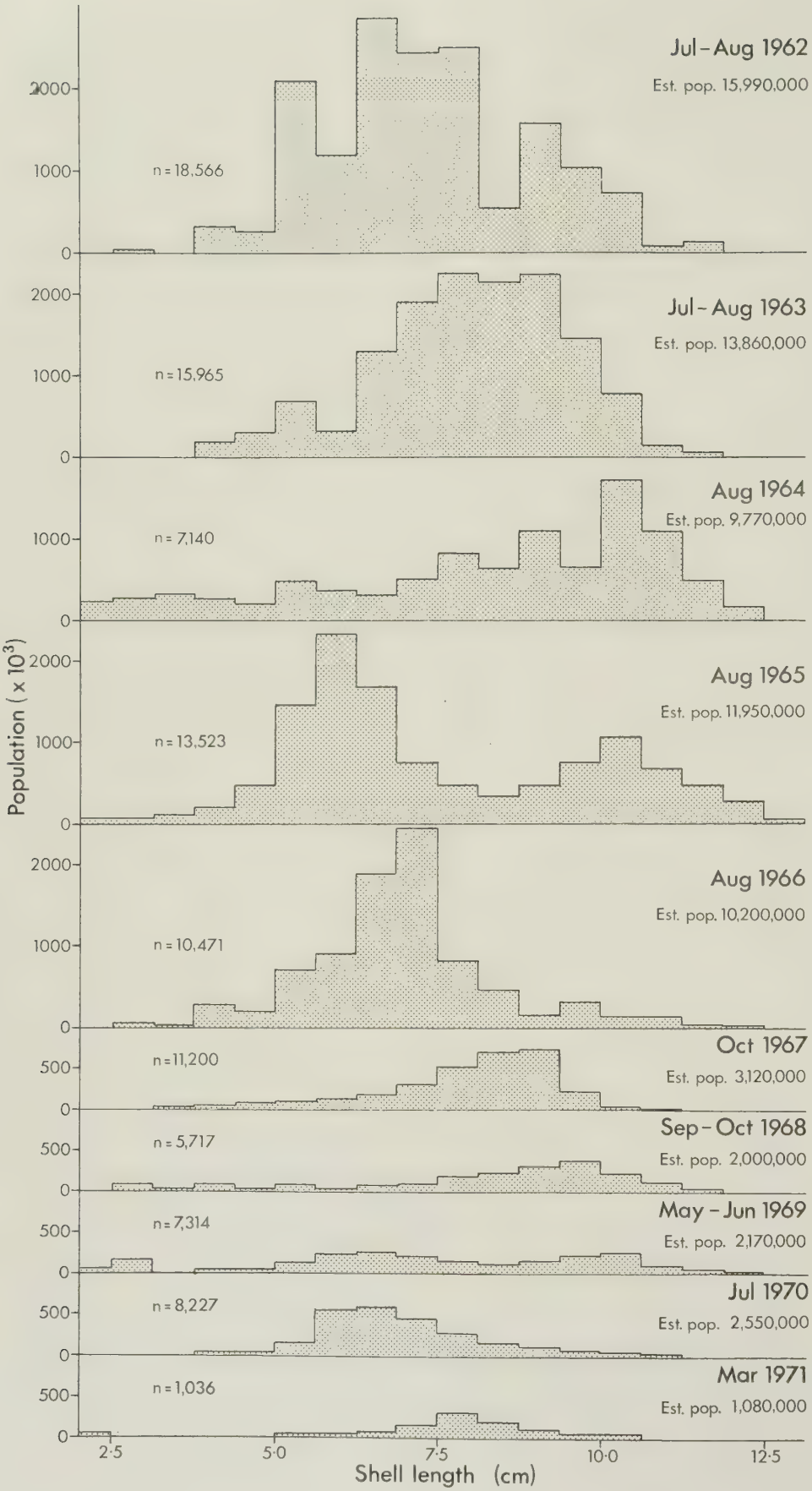


Fig. 15: Total population shell length-frequency distributions, Dargaville beach, from 1962 to 1971. Data from Meredith Bros. surveys.

GROWTH

There is a linear relationship between any two parameters of shell length, width, or depth (Fig. 7). In this bulletin the shell length has been used as the major growth parameter.

Frequency distributions of the shell length of samples of populations generally displayed only one or two modes that could be attributed to year groups (Fig. 15). When such modes occurred they usually corresponded to the first- and second-year groups. In the remainder of the population the ranges of length in year groups overlap because the growth increments in succeeding years are fairly small or because of the protracted settlement period. Thus the subdivision of a toheroa population into year groups must be somewhat arbitrary.

For the first 18 months after spatfall advantage can be taken of the post-setting behaviour of the juveniles. Up to this time the juvenile populations are largely separated from the rest of the population either because they occupy different levels of the beach or because they form mono-age-group beds.

During the study period most of the spat settled on the beach between November and March, which made a difference of 6 months between the oldest and youngest individuals. In 1969 and 1970 samples of the juveniles recruited during the 1968–69 season were collected about once a month, measured, and returned to the beach. Similarly, samples were collected at intervals of 2 months from the following reproductive season, 1969–70. Sample numbers generally ranged from 50 to over 200.

Frequency distributions of the shell length at 2-monthly intervals for the 1968–69 recruits and for the 1969–70 recruits are shown (Fig. 14). The more or less normal distributions from May to November 1969 for the 1968–69 recruits indicated that the sampling technique encompassed the whole population. The January to November 1970 distributions for the 1969–70 recruits also showed that the first- and second-year group populations were almost completely distinct, though in years when the period of the spatfall was even longer the populations could possibly overlap.

The shell length-age relationship for the first 18 months after spatfall is shown (Fig. 16). The standard deviations for the 1968–69 recruits are also

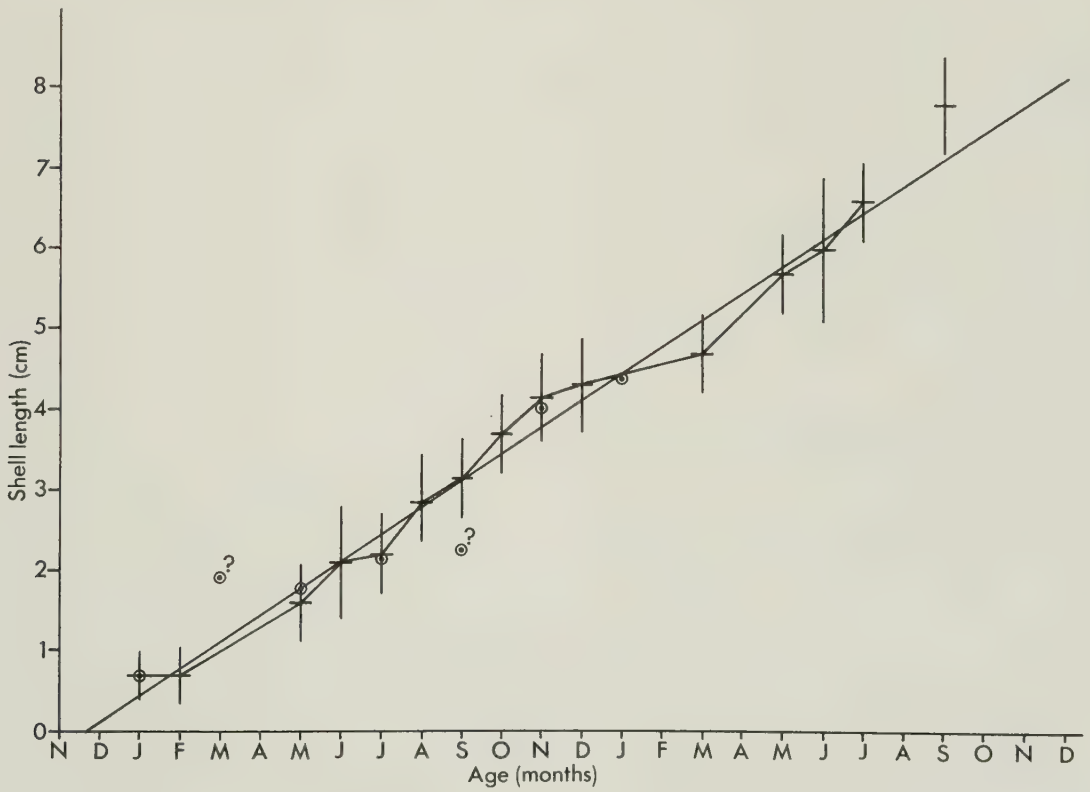


Fig. 16: The shell length-age relationship of juveniles. The 1968–69 spatfall is indicated by joined points and the 1969–70 spatfall by circles. The slope has been calculated.

TABLE 4: Shell length-age relationship on Dargaville beach, compared with results of Cassie (1955) and Rapson (1952)

Age (years)	Shell length from intermediate bands* n	S.D.	Mean (cm)	Aged shells† n	S.D.	Mean (cm)	Cassie (1955) Mean (cm)	Rapson (1952) Mean (cm)
0.5	—	—	—	163	0.56	2.18	—	—
1.0	190	0.75	4.92	126	0.89	4.24	4.7	4.2
2.0	177	0.77	7.11	72	1.26	6.99	6.5	6.8
3.0	159	1.32	8.66	307	0.79	9.08	8.1	9.6
4.0	137	0.64	9.64	249	0.55	9.89	9.4	11.0
5.0	96	0.83	10.48	446	0.59	10.64	10.5	11.7
6.0	59	0.52	11.14	208	0.51	11.17	11.3	12.4
7.0	10	0.62	11.58	31	0.38	11.73	11.9	—

* Shell length data derived from the measurement of inter-median rings. See page 12.

† Aged shell data from the measurement of aged shells.

indicated. Though several growth checks were apparent during this period, the general trend was towards linear growth. The slope has been calculated for the 1968–69 recruits, and the correlation coefficient for a sample number of 18 is 0.988, significant at a probability level of P = 0.05. From this slope the relative growth during this period was 0.33 cm per month or about 4.0 cm per year. Some of the later growth checks appear to be correlated with periods of gonadal development, but this relationship has not been fully established.

Growth data for toheroa over 18 months have been obtained from the measurement of shells in relation to their "annual" bands by the method outlined on page 12: (a) the measurement of the length of aged shells and (b) the measurement by shell reading of the length at each successive year.

Lengths of 1,602 shells of known age were measured during the study period. From these a subsample of 190 shells of different ages was selected for shell reading measurements. The results of these measurements are given (Table 4) with their standard deviations for the ages 1 to 7 years. These results are

TABLE 5: Comparison between growth increments derived from marked specimens and those derived from the length-age relationship

Year group (years)	Marked specimen growth increments n	Mean (cm)	Length-age relationship growth increments (cm)
1-2	1	2.3	2.8
2-3	10	1.3	1.6
3-4	15	1.0	1.0
4-5	17	0.8	0.8
5-6	16	0.6	0.6
6-7	6	0.4	0.6

The marked specimens were returned at various time intervals after being replaced on the beach.

The yearly growth increments are extrapolated values derived from the length increases recorded.

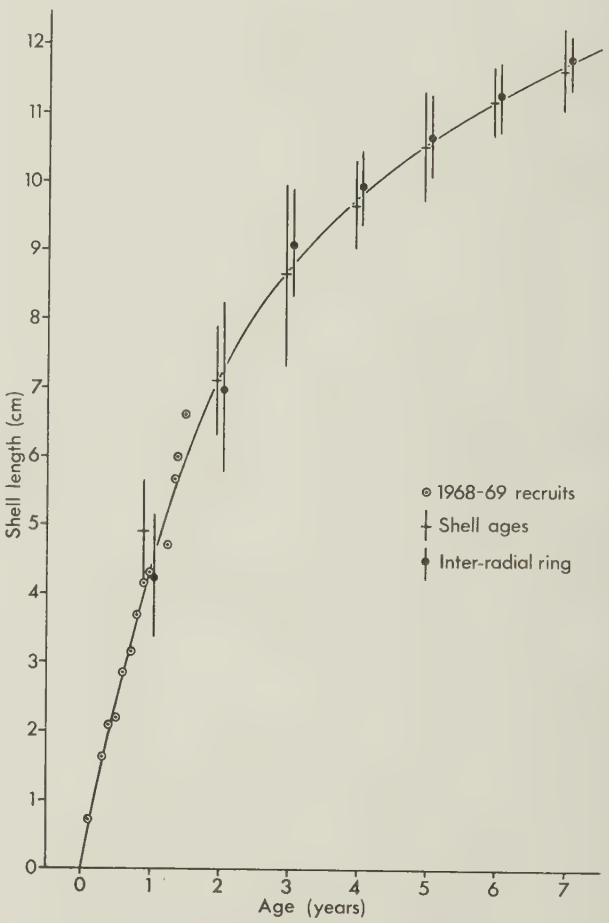


Fig. 17: The shell length-age relationship of adults.

also compared with those derived by Cassie (1955) and Rapson (1952). There is reasonable agreement between the lengths determined during the present study and those determined by Cassie.

A composite growth curve has been established by combining the results obtained from the periodic measurement of juveniles and from the shell ages

and the shell readings of adults (Fig. 17). From this curve the average length at the end of each year is:

Age (year)	Average length (cm)
1	4.3
2	7.1
3	8.6
4	9.6
5	10.5
6	11.2
7	11.7

The Ministry of Agriculture and Fisheries regulation size limit of 3 in. (7.6 cm) is attained early in the third year.

Some corroboration for the growth curve has been derived from the return of some marked toheroa. At various time intervals after marking, some 65 individuals have been returned. The shells of these animals were aged and measured, and the increase in length recorded was extrapolated to give the annual growth increment. These results are given (Table 5) and compare favourably with those derived from the growth curve.

POPULATION DENSITY AND STRUCTURE

Before 1962 surveys of the beach populations of toheroa were not made regularly. The available data since 1933 have been summarised (Table 6). Most of these surveys were conducted on Muriwai Beach by Rapson (1954) and Cassie (1955), the former between 1937 and 1943 and the latter in 1948 and 1949.

In 1962 the Marine Department began a programme of annual surveys of the major beach populations on the North Auckland Peninsula (Greenway 1969, 1972). A similar programme was begun on the Wellington west coast beaches in 1965 (Tunbridge 1967, 1969; Williamson 1969a, 1969b, 1970) and on the South Island beaches in 1966 (Street 1971). The survey techniques are summarised (page 11). The North Auckland and the South Island beaches have been surveyed twice a year, before and after the open season, and the Wellington beaches have been surveyed once a year, before the season.

Meredith Bros. also began a programme of annual pre-season surveys of the toheroa on their concession on the southern half of Dargaville beach in 1962.

TABLE 6: Estimates of population, in millions, on principal beaches, 1933-60

Year	Ninety Mile	Dargaville	Muriwai	Wellington (Waitarere and Hokio)
1933	11–12*	—	—	—
1935	—	—	—	2.5†
1937	—	—	15	—
1938	—	9.1	4 (1)‡	—
1939	12.0	—	—	—
1940	—	—	5	2.5*
1941	—	—	5	—
1942	—	—	5*	—
1943	—	—	5§	—
1944	Scarce	—	—	—
1945	Scarce	—	—	—
1946	6	—	—	—
1947	—	—	3§	—
1948	Very scarce	5	10 & 13‖	0.7¶
1949	—	—	15	—
1950	—	—	1§	—
1951	—	—	—	0.3
1952	—	—	8	—
1955	—	10	—	0.3
1957	6.2	—	—	0.2

* Over 3 in. (7.6 cm) only.

† Waitarere only.

‡ Value in parentheses after mortality.

§ Only part of beach surveyed (about half).

‖ Two surveys.

¶ Hokio only.

Data sources: Cassie (1955), Rapson (1954), Marine Department archives.

TABLE 7: Comparison between the Marine Department and Meredith Bros. surveys over the same section of Dargaville beach

Year	Month	Marine Department (millions)	Month	Meredith Bros. (millions)
1962	September	14.95	July-August	15.99
1963	September	10.52	July-August	13.86
1964	October	9.63	August	9.77
1965	November	12.43	August	11.95
1966	April	10.54	July-August	10.20
1967	October	3.16	October	3.12
1968	April	3.83	September	2.00
1969	April	4.39	May-June	2.17
1970	May	6.47	July	2.55
1971	May	—	March	1.08

Data sources: Greenway (1969, 1972), Meredith Bros. unpublished records.

Their survey technique is described (page 12). These surveys were designed to provide information regarding the population distribution and abundance of toheroa in each bed in the concession area so that the cannery could select those most suitable for harvesting during the open season. The data also provide information on the changes in the population with time on this part of the beach. Before 1967 the data gave information regarding the position and area of each bed and the length-frequency distribution for each $\frac{1}{2}$-mile (800-m) section of the beach as well as an estimate of the total population of the concession. After 1967 the survey procedure was changed to give estimates of bed populations also.

It is difficult to survey toheroa populations with any degree of accuracy. Allen (1962) analysed the data from the Marine Department October 1961 survey of Ninety Mile Beach. His best estimate was 7,800,000, with a range of 4,600,000 to 13,400,000. Greenway (1969) conducted simultaneous surveys of Muriwai Beach in February 1964 and gave estimates of 7,400,000 and 12,400,000, with a mean of 9,900,000. The Meredith surveys are also subject to similar errors; 95% confidence limits for individual beds may range from $\pm$ 25 to 100%. However, the population estimates obtained by Meredith Bros. on the southern half of Dargaville beach compare favourably with those determined by the Marine Department for the same area (Table 7).

Juvenile toheroa under 1 year old (less than 2.5 cm) are consistently under-represented in the length-frequency distribution produced from all the survey data. Street (1971) pointed out that unless the sand from the quadrats or transects is sieved, many errors will be involved. Depending on the time of

the survey, the juveniles may also be spatially separate from the rest of the population and may either be diffusely distributed over the littoral zone or be concentrated into a narrow band at a distance from the adult bed (page 29). The spatfall is also highly variable both in time of occurrence and in endurance. To estimate the juvenile population, several surveys over the entire littoral zone would have to be conducted each year. However, this part of the population is generally partially surveyed in the post-season surveys of each year and totally surveyed in the pre-season survey of the following year.

The Marine Department population estimates since 1962 are shown for the major beaches in New Zealand (Table 8). Since 1962 there has been considerable fluctuation in the population on the North Auckland beaches, with a general tendency towards a population decline. There is a slight tendency for the population fluctuation to decrease from north to south:

	Total population (millions)	Population/mile of beach (thousands)
Ninety Mile Beach	1 to 40	15 to 800
Dargaville beach	3 to 20	100 to 600
Muriwai Beach	1 to 10	23 to 300

Good recruitment to the beaches has been irregular and was not apparent on all beaches during the same time interval. For example, in 1963 Ninety Mile Beach had a reasonable settlement, but the spatfalls on Dargaville and Muriwai were poor by comparison.

The Wellington west coast beaches have apparently never had large populations compared with those in North Auckland. The combined populations of Waitarere and Hokio Beaches have rarely exceeded 1,000,000. The recruitment to these beaches is very irregular; in 1971 the population consisted almost totally of older animals. In 1965 Tunbridge (1967) noted that there was a substantial population of small toheroa. Judging from the size of these small animals they must have been between 1 and 2 years old, so that spatfall must have occurred between 1963 and 1964. There has apparently not been a successful spatfall since then.

Since surveys were started on the South Island beaches in 1966 the Te Waewae Bay population density has remained fairly constant between 1,900,000 and 2,500,000, with a more balanced age structure, which indicates some recruitment by spatfall in most years. The presence of a significant proportion of older animals in the group over 12.5 cm long (eighth-year group) suggests that until recently this population has been fairly lightly exploited. But the recent opening of a new road access to the area has led to a greatly increased exploitation.

TABLE 8: Estimates of population, in millions, on principal beaches, 1961-71

Year	Time of survey*	Ninety Mile	Dargaville	Muriwai	Wellington (Waitarere and Hokio)	South Island (Te Waewae)
1962	b.s.	—	—	—	—	—
	a.s.	25.0	20.5	5.2	—	—
1963	b.s.	26.2	—	4.7	—	—
	a.s.	37.0	18.1	8.3	—	—
1964	b.s.	22.1	10.9	7.4 (12.4) §	—	—
	a.s.	13.5	14.8	—	—	—
1965	b.s.	5.6 (1.5)†	7.3‡	1.6‖	0.8	—
	a.s.	3.9	15.4	3.6	—	—
1966	b.s.	2.3	11.8	5.4	0.8	2.4
	a.s.	1.9	14.6	3.1	—	2.5
1967	b.s.	0.5	3.3	2.3	—	2.2
	a.s.	0.8	5.1	3.8	—	1.9
1968	b.s.	1.9	6.3	6.7	0.8	2.5
	a.s.	6.9	3.4	2.2	—	2.2
1969	b.s.	7.0	6.5	3.8	0.5	1.9
	a.s.	9.3	8.1	2.6	—	2.0
1970	b.s.	18.4	11.2	2.6	0.1	2.0
	a.s.	41.0	8.2	0.7	—	—
1971	b.s.	10.4	3.2	1.4	0.04	1.5

* b.s.: before season.
a.s.: after season.
† 2 pre-season surveys.
‡ 10 miles only.
§ Simultaneous surveys.
‖ 1 section not surveyed.

Data sources: Greenway (1972), Tunbridge (1967, 1969), Street (1971), Williamson (1969a, 1969b, 1970, 1971), Marine Department archives.

The Meredith Bros. survey data for the southern end of Dargaville beach indicate the change in the population distribution since 1962. The number of toheroa sampled in each 800-m section of the beach is proportional to the population in that section. The number of toheroa sampled in each section has been expressed as a percentage of the total number of animals dug over the whole length of the beach (Fig. 18).

The survey areas begin 1.6 km south of Glinks Gully at the major road entrance to this part of the beach. There are two other vehicle access points, further south, but these are suitable only for four-wheel-drive vehicles or tractors. Four streams traverse the littoral zone in sections 2, 5, 10, and 28. Few toheroa have been found south of section 28, which is influenced by the water flowing into and out of the Kaipara Harbour, and the substrate is much less stable than that in more northern parts of the beach.

In 1962 the population was more or less uniformly distributed along the beach, though there were some larger aggregations in sections 9 and 16. By 1963 the population had declined in sections 11 to 15. This was followed by a general decline of the northern sections from 1964 to 1966, except for good

beds in sections 2, 5, and 10. This was followed in 1967 by a decline on the southern end of the area from section 25 on. These conditions persisted until the spatfall in 1968–69, the juveniles from which eventually colonised the mid-tide level and were indicated in the 1970 survey. The northern half of the area was recolonised in sections 1 to 10, but 11 to 14 remained relatively depleted. In sections 6 to 9 several mono-age-group beds were formed, but these declined during the following year, 1970–71.

The inclination of the substrate at right angles to the beach is greater on the northern end apart from those areas immediately adjacent to streams (sections 2, 5, and 10). This is probably due to a build-up of beach material and subsequent scouring which possibly started in sections 11 to 15 in 1962 or 1963. Greenway (1969) also noted that in 1967 there was some extensive beach scouring. However, the inclination in areas close to the streams appears to have been fairly constant owing to the streams

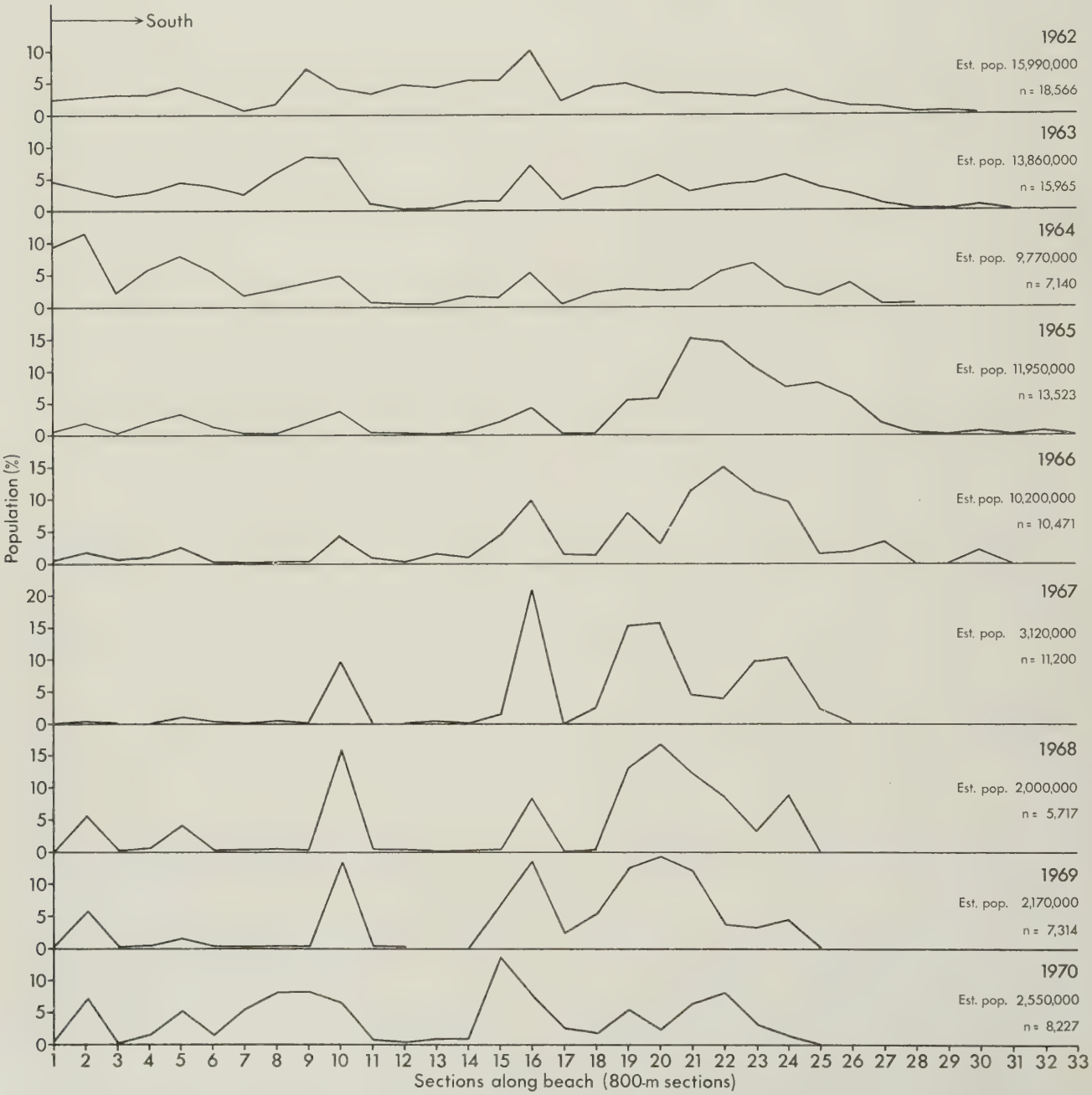


Fig. 18: Population distribution per 800 m along the southern half of Dargaville beach south of Glinks Gully.

pushing out deltas of sand which tend to produce broad, low-lying areas.

During the study period surveys were conducted on two beds in sections 2 and 10 at 2-monthly intervals. This programme was begun on the bed in section 10 in July 1969 and the bed in section 2 in March 1970 and continued until July 1970. The surveys were terminated when it was realised that both bed populations were declining rapidly, but a check survey was carried out on both beds in March 1971. There may be some correlation with digging activity (sand disturbance) and the population decline, but this aspect has not been investigated.

Total population length-frequency distributions for these beds have been extrapolated from the survey data and are shown (Fig. 19).

During the experimental period there was a complete change in the population structure. This is more readily seen from the distributions for the bed in section 10. The total population of this bed increased from July to November 1969 with the immigration of juveniles from the upper levels of the beach. There was a corresponding increase in bed area from about 10,000 sq m to 18,000 sq m. However, there was also a decrease in the numbers of adults of over 10 cm long during the same period. Numbers in the mid-size range (about 7 cm) stayed fairly stable.

Part of the adult decline may be attributed to the public and cannery harvest during the open season in the last 2 weeks of September, but the decline before the open season from July to early September was almost as great as the decline from September to November. Between November 1969 and January 1970 there was some sand movement and the beach was built up in this area (up to 30 cm). The bed area increased to 40,000 sq m and there was a general decline in the whole population which continued until July 1970. The juvenile population declined from an estimated 442,000 in November 1969 to 120,000 in July 1970. During the same period the adults declined from 144,000 to 16,000. The bed area decreased to 5,000 sq m and split into two small beds. The decline in toheroa over 10 cm long was most pronounced. In January and February 1971 there was a general mortality of toheroa on the beach (see page 42), and by March 1971 the total population had declined to 64,000. There were very few toheroa over 10 cm long. The bed area had also fallen to 2,000 sq m.

These population declines cannot be assigned to exploitation, especially in the juveniles, and must result either from mortality or from emigration. The deposition of empty toheroa shells at the top of the beach, including marked shells that had been replanted in this bed, during the survey period indicated that some mortality was occurring during most months. Attempts to estimate absolute mortalities by counting empty shells deposited along the strand line were inconclusive.

Initial searches for off-shore toheroa have also been inconclusive (see page 20). However, some form of along-shore movement may occur. Along-shore movement of young toheroa was indicated during the first 2 years after settlement (page 31). Data from the Meredith Bros. beach surveys also tend to support this. If the length-frequency distributions for any bed are compared from one year to the next, occasional population increases may be noted, which consist of animals from the second-year and older groups. These increases cannot be assigned to recruitment by spatfall and must be due to the immigration of toheroa. Similarly for the years 1963 to 1966 there is a weak correlation between the mean length of the population in each 800-m section of the beach and the distance along the shore, so that the mean length of the toheroa decreases from north to south. The correlation coefficients for these examples ranged from 0.405 to 0.831 (sample numbers 28 to 33) and were thus significant at a probability level of $P = 0.05$.

Mestayer (1921) suggested that toheroa may migrate along the coast in accordance with the set of the in-shore ocean currents. Her account of such migrations was based on hearsay evidence and is similar to that reported to the author by various surf fishermen in the Dargaville beach region.

From these accounts it would seem that mass migrations of toheroa are likely to occur in summer during periods of calm seas and weather. Many toheroa (most accounts indicate thousands) may then emerge from the beach into the swash or backwash of a wave. There they allow themselves to be carried across the beach in the surf until they eventually resettle during the period of slack water between two succeeding waves. That such migrations have not been observed during winter may be explained by the fact that surf fishing is largely a summer recreation.

Such movement of adult toheroa has not been observed during nocturnal vigils on the beach, but down-shore movement of juveniles on an ebbing tide has been observed several times. The small toheroa release themselves from the substrate into the backwash of a wave and are carried down shore to resettle quickly during the interval of slack water. Observation of occasional adult toheroa suggests that the animal emerges from the sand by pushing down with the foot, but its subsequent movement over the beach appears to be a passive transport by the surf.

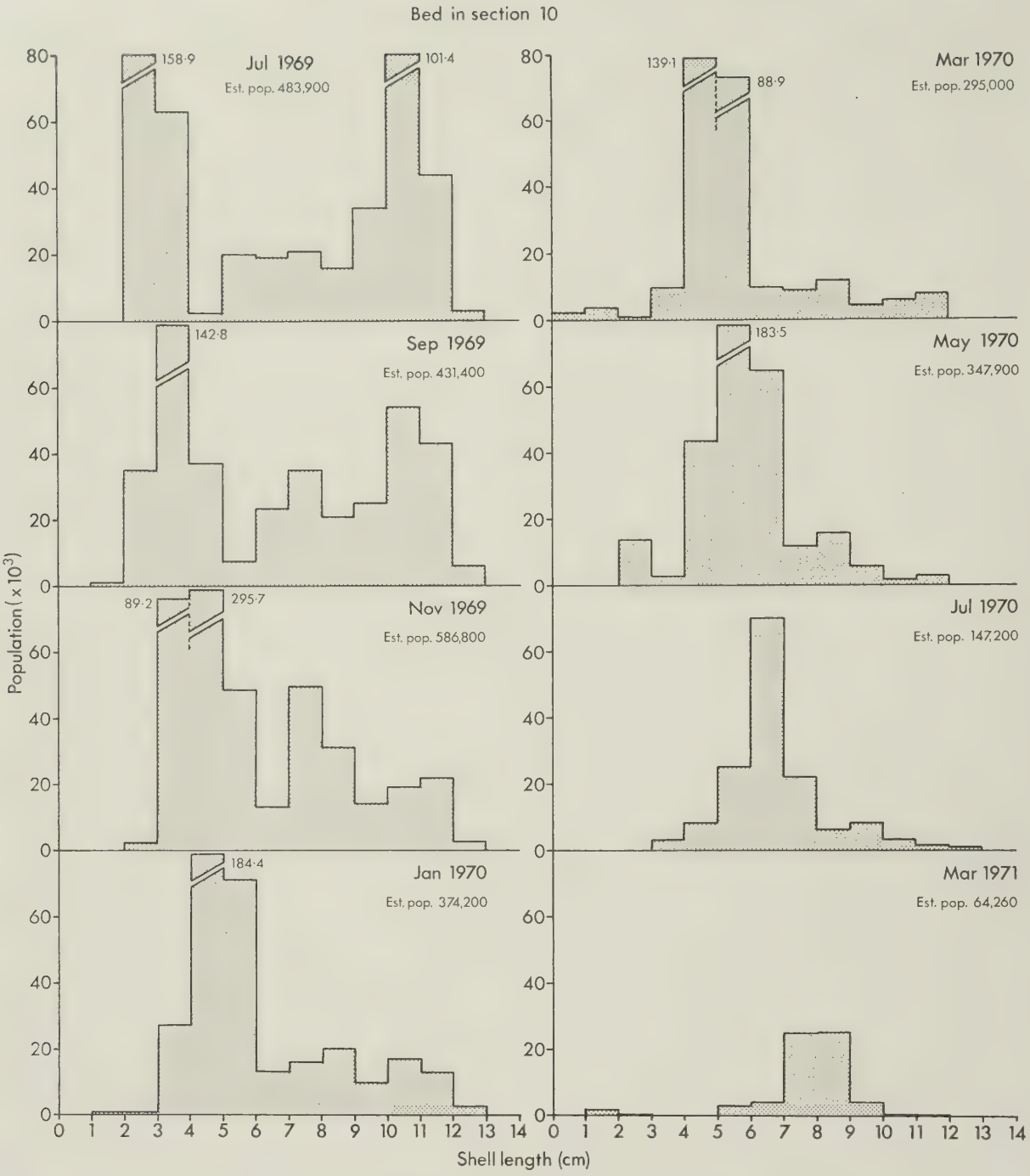
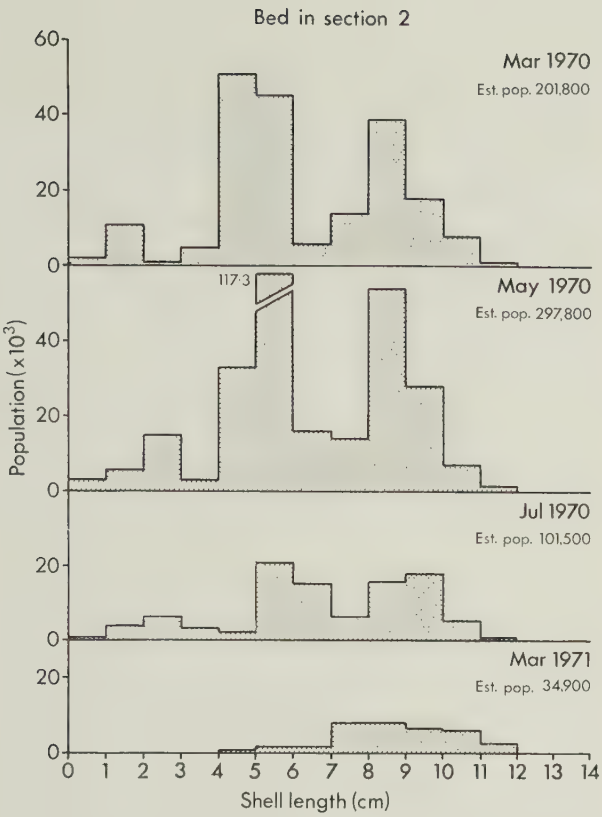


Fig. 19 (above and right): Total population shell length-frequency distributions of two beds in sections 2 and 10 respectively at 2-monthly intervals until July 1970, with a final survey in March 1971.

Some animals were seen to be carried up and down shore several times before they attempted to bury into the sand, and some of these toheroa finally reburied themselves very near to their point of emergence. During the time that the toheroa were carried up and down shore by the surf the siphons and feet were extended in some animals to act like keels to stabilise themselves and allow them to float more or less evenly. In others both organs were fully retracted into the shell and the toheroa were rolled willy-nilly by the surf.

Toheroa kept in aquariums in the laboratory have been recorded as being more active at night than during the day. At night the siphons are often



extended well above the sand surface and the animals pump vigorously. Many emerge from the sand by firmly pushing down with the foot so that they almost jump out of the substrate. This process is similar to that described for *Mactra olorina* (Philippi) by Ansell and Trevallion (1969). Small toheroa were much more likely to emerge than adults. During the day the animals rarely emerged from the sand, and the siphons were seldom extended beyond the sand surface.

The total length-frequency distributions for the population on the southern half of Dargaville beach have been calculated for the years 1962 to 1971 from the Meredith pre-season survey data (Fig. 15). The first-year group is not fully represented for the reasons given above.

The fairly large population until 1966 was derived from three periods of settlement that probably occurred during the 1960–61, 1961–62, and 1963–64 reproductive seasons. This has produced distributions which consist largely of first- or second-year groups and are similar to those described for *Donax gouldi* (Dall) by Coe (1953).

Observations during the 1968–69 reproductive season suggested that the settlement had been relatively heavy, and by June 1969 the juvenile population on the Meredith concession was estimated to be 2,250,000 (density 17 per square metre). By July 1970 the Meredith survey distribution (Fig. 15) indicated that this population was reduced by some 50%. To produce the population peaks indicated in 1962, 1963, and 1965 the settlement must have been larger and/or longer than that observed in 1968–69 or the mortality during the first year must have been minimal during those years.

The fairly small population after 1966 resulted from a sudden loss of toheroa from the beach between 1966 and 1967. The reasons for this are uncertain. Exploitation rates before 1967 were fairly high, and there are some unconfirmed reports that the harvest in 1966 was the heaviest in recent years. However, the Marine Department survey results (Table 8) indicate that the loss occurred between October 1966 (after the open season) and April 1967 (when the surveys were made). If it is assumed that these values are correct (and there has generally been good correlation between the Meredith and Marine Department surveys) then the loss to the population must be due to either an off-shore migration or mortality. The presence of an off-shore population has yet to be confirmed and appears unlikely. However, there is no report of any mortality in the literature. Greenway (1969) observed evidence of large-scale beach scouring in July 1967 and the presence of numerous toheroa shells littering the southern end of the beach. A similar sudden change in the beach level during the early part of the year may have removed a large proportion of the population.

MORTALITY

Rapson (1952) lists some of the predators of toheroa to be the red-billed gull, *Larus novaehollandiae scopulinus,* the black-backed gull, *Larus dominicanus,* and the snapper, *Chrysophrys auratus* (Bloch and Schneider). Street (1971) also lists oystercatchers, *Haematopus* spp. The rough skate, *Raja australis* Macleay, and the short-tail sting ray, *Dasyatis brevicaudatus* (Hutton), may possibly be added to the list, as they are commonly found in the shallow coastal waters adjacent to toheroa beaches. So, too, may the swimming crab, *Ovalipes catharus,* which occupies the level of the shore just below low water and has been observed to attack toheroa if they are carried down shore by the surf.

Waugh and Greenway (1967) found stranded toheroa shells that they suggest may have been drilled by gastropods, possibly *Phalium* (*Xenophalium*) *pyrum pyrum.* These gastropods have been found only in the sub-littoral during the experimental period, but it is likely that even if there is no off-shore migration of toheroa, some will be carried off shore during periods of beach upheaval.

Apart from nibbling at the exposed tips of the siphons all these predators would have difficulty in excavating deeply buried toheroa. However, juvenile toheroa emerge from the sand during their downshore migration, and occasional adults have also been observed to emerge from the sand to be carried by the surf. Such movement may occur often, as beds on the beach have been noted to change position and form from month to month. Heavy vehicular traffic also semi-liquefies the sand, and the toheroa are floated up towards the sand surface, where a small hummock is pushed up (Fig. 20). This may cause the animals to be leached out of the sand by the surf during the next high tide. During and after periods of beach material upheaval by the surf considerable losses to the population are apparent from the numerous shells left stranded above the high water mark with shreds of meat still adhering to them. Gulls have been observed to excavate toheroa close to the sand surface.

No endemic diseases of toheroa have been reported, but occasional mass summer mortalities do occur. Rapson (1954) recorded a summer mortality on all the North Island beaches in 1938, and Meredith Bros. Ltd. recorded similar occurrences on Dargaville beach during the summers from 1956 to 1959. The mortality of toheroa on all the North Auckland beaches in February 1971 appears to have been similar.

Rapson (1954) observed that the toheroa remained

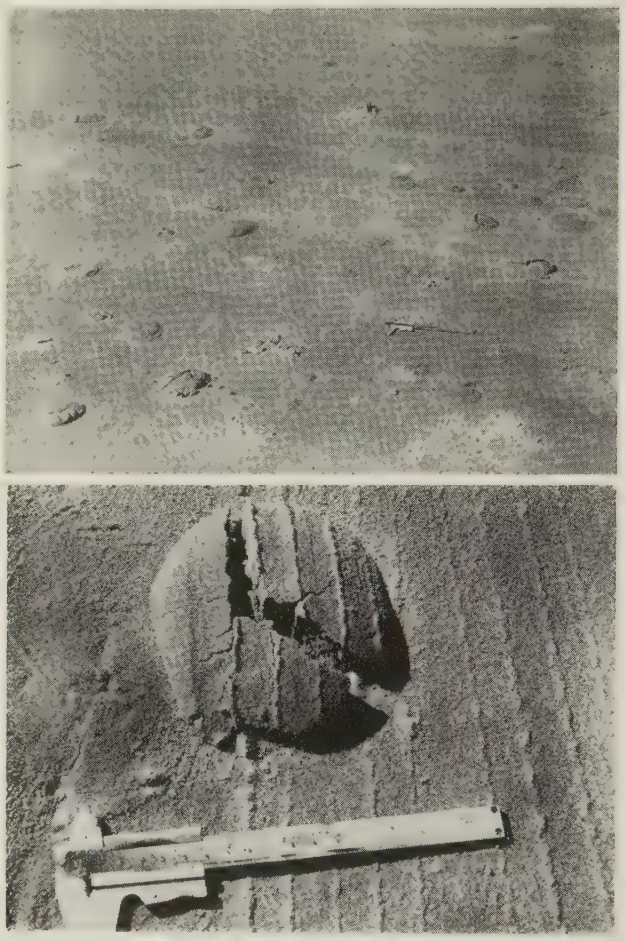


Fig. 20: Hummocks caused by toheroa being floated in sand liquefied by the passage of vehicular traffic.

half exposed and that they were lethargic before death. The siphons were extended and the animals made only feeble attempts to dig into the substrate. They did not respond to external stimuli such as pricking the siphons, mantle, or the foot. He considered that this condition was due to a lack of oxygen and heat stress resulting from calm surf conditions and the fact that the tide did not cover the levels occupied by the toheroa for several days. The situation was also aggravated by the animals' poor condition through spawning.

In February 1971 the amplitude of the tide was apparently reduced by persistent off-shore winds. This reduction was sufficient during periods of neap tides to leave the mid-tide region of the beach uncovered for several days. These conditions also coincided with a period of high air temperature and high insolation, which resulted in a mortality of considerable importance. In some areas the tide covered half an aggregation of toheroa and those

that were submerged for a short period were not as adversely affected as those above the tide level. The effects at Dargaville beach were more pronounced on the southern end of the beach, which is backed by sand dunes. Drifting sand from these dunes may have raised the level of the beach further so that larger areas were exposed during the period of reduced tides. The estimated loss to the population on two $\frac{1}{2}$-mile sections on the southern end of the beach was 134,300 and 169,000 (91% and 92% respectively), compared with 97,800, 6,000, and 46,400 on three more northern sections (66%, 4.8%, and 28% respectively).

Mackin (1959) proposed that survival curves could be produced directly from the length-frequency distributions for bivalves provided that the annual rate of recruitment was regular. As the rate of recruitment to a toheroa population is highly variable, this technique cannot be applied directly. However, the approximate numbers in each year group in a length-frequency distribution can be extrapolated with reference to the total population estimate and the growth increments derived from the growth curve. The decline in numbers of a single year group can thus be traced over a period of years from the annual survey data.

By use of this technique survival curves for the year groups that settled from 1961 to 1966 have been established from the end of the first year to the fifth or sixth year. These curves are shown (Fig. 21). The first-year group is omitted for the reasons given earlier. These curves are compared with curves projected for assumed populations with mortality rates of 30 to 80% per year. In general the mortality ranges from 40 to 60%, with a mean of about 50% per year. The change in inclination of any part of a curve indicates the change in the survival rate from one year to the next. For example, the population decline from 1966 to 1967 is indicated by the steeper inclination in the curves for toheroa that settled in 1962 to 1965.

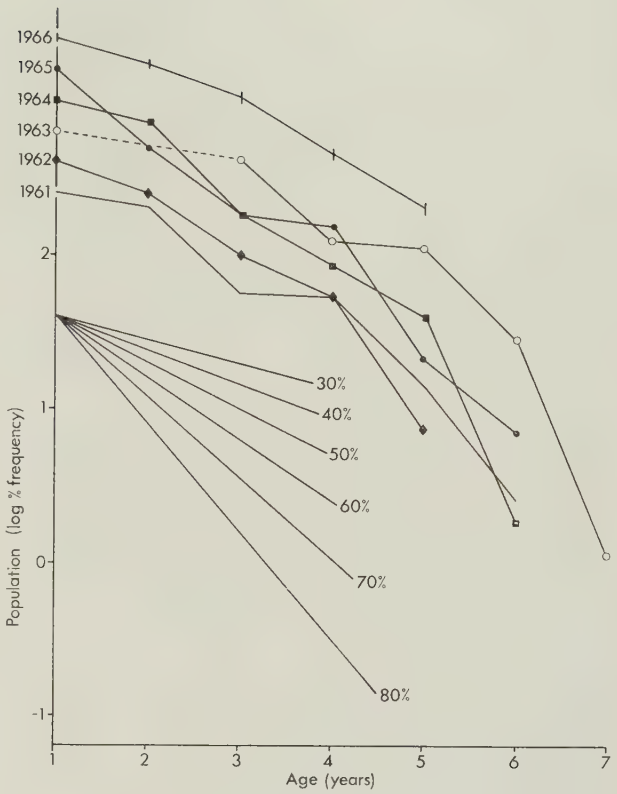


Fig. 21: Extrapolated survival curves for the second- to sixth-year groups, with curves for assumed populations at various mortality rates.

Similar extrapolation of data for first-year animals derived from the 2-monthly bed surveys in sections 2 and 10 gave survival rates of 26% and 30% per year.

These values represent total survival rates. Attempts to establish natural and/or exploitation rates have not been successful. An account of the recorded exploitation rates has been given in the section "Exploitation".

DISCUSSION

A prolonged breeding habit may be characteristic of bivalve molluscs that colonise sand beaches in regions where the annual temperature range is small. Coe and Fitch (1950) showed that *Tivela stultorum* Mawe at La Jolla, California, had a breeding season of 7 to 8 months from June to December or January and that a few animals might spawn intermittently during the rest of the year. The annual temperature range is 8°, from 13 to 21°C. Coe (1955) also recorded that in the same region *Donax gouldi* bred for a similar period from April to October or November. *Donax denticulatus* breeds throughout the year, with a peak spawning period from November to January in the West Indies (Wade 1968). Alagarswami (1966) recorded that the breeding season for *Donax faba* Gmelin on the beaches around Mandapam in India extends over 8 months, from November to June. There are two peaks of spawning, from November to December and from May to June. The annual temperature range is 4°, from 26 to 30°C. Rao (1967), working on *Donax cuneatus* Linnaeus on the Madras coast of India, recorded that the breeding season was for 7 months, from December to June, and that the temperature range was 6°, from 26 to 32°C. In the present study toheroa have been shown to be capable of breeding throughout the year, with a peak of spawning from November to February. The temperature range is 8°, from 14 to 22°C.

Temperature has been cited as the most important factor controlling the emission of gametes, but those molluscs which live in warm temperate to tropical climates are subject to a fairly narrow temperature regime. Ropes (1968), during his study on the reproductive cycle of *Spisula solidissima* from New Jersey, suggested that temperature was not clearly a stimulus to spawning. Wilson and Hodgkin (1967) made a comparative study of five species of mussel near Fremantle, Western Australia, and indicated that though temperature was the controlling factor in reproduction, other factors must be important. The reproductive cycle in the toheroa is continuous unless the animal is deprived of a plentiful supply of nutrients. There is some indication that the gonad can be cycled from ripe to partially spawned and back to active gametogenesis within 1 month. In some of the material examined several stages of the reproductive cycle could be observed in a single gonad; some follicles were ripe and others were in the spawned or active condition. The controlling factor for the toheroa appears to depend on the supply of nutrients; as Rapson (1952) succinctly states: " . . . when toheroa in northern waters are fat they spawn".

The migratory behaviour of intertidal molluscs on sandy beaches has been recorded by various authors: Jacobson (1955), Turner and Belding (1957), Edgren (1959), and Wade (1967). Ansell and Trevallion (1969) reviewed the subject and considered that for such movements to occur the animals must be capable of rapid response. They concurred with Wade (1967) that the up- and down-shore movements of various species of *Donax* with the tide cycle were non-tidal in character and that the migration did not require any form of intrinsic rhythm mechanism.

The up-shore movement of juvenile toheroa after setting is probably caused mechanically by the action of the surf. Small toheroa less than 0.5 cm long cannot secure a firm purchase in the substrate and can be floated out of saturated sand with gentle agitation. The swash of succeeding waves probably washes the young toheroa out of the sand and sorts them towards the high water mark. However, the subsequent down-shore and horizontal sorting of the juveniles is partly voluntary in that the animals emerge vigorously from the sand into the waves. There is also some movement in the adult beds in that the area occupied by the toheroa and the position relative to the mid-tide level may show considerable fluctuation. Such movements may also be partly voluntary.

The emergence response may be controlled by the degree of saturation of the sand that the toheroa is left in when it is not covered by the tide. If the sand is fairly dry, the next wave that passes over the animal may stimulate it to emerge. Emergence must also be controlled by some light threshold, as these animals generally do not emerge during daylight. The response may thus be used by the juveniles to move down shore to the mid-tide level and by the adults to maintain their position in damp sand. That the response is some form of escape mechanism is shown by the fact that several toheroa have been observed with shells malformed by crowding, which indicates that they have not moved for a long time (see also Rapson 1952).

On the basis of several random surveys Cassie (1955) postulated a sub-littoral population of toheroa to explain two points in his data. The first was that the age composition of toheroa on both Muriwai Beach and the Wellington west coast beaches appeared to represent an incomplete portion of some larger population and the second was that the populations showed large fluctuations. The missing portion of the age composition occurred largely in the first and second years. Waugh and Greenway (1967) proposed that stranded shells on the shore apparently drilled by boring gastropods may have derived from

a sub-littoral population, as such gastropods have not been found on the shore.

Attempts have been made to find sub-littoral populations; Street (1971) investigated the sea bed off Te Waewae Beach with divers and found no sign of a sub-littoral population. On Dargaville beach commercial harvests of tuatua, *Paphies* (*Mesodesma*) *subtriangulata subtriangulata*, have been taken from the immediate sub-littoral during the last 2 years and have been examined on several occasions by the local fisheries inspector and no toheroa have been found (D. J. Young pers. comm.). Finally during the experimental period samples of the sub-littoral fauna were collected by dredging off Dargaville beach up to 1.6 km off shore. Live toheroa were not collected in these samples, but some fragments of subfossil toheroa shell were dredged up similar to those described by Cassie (1955). If a sub-littoral population or populations exist, it is considered that they must be either concentrated or further and deeper off shore.

However, on the basis of more extensive surveys carried out since Cassie's work the structure of the populations could be explained by the phenomenon of resurgence as defined by Coe (1953). Extrapolation of the survey data shows that the second-year groups are more or less fully represented in the distributions and the first-year groups are absent from them because generally they were not fully sampled during the surveys. The large fluctuations in population are due then to periods of highly successful settlement followed by periods of poor settlement and a fairly high mortality rate, so that the distribution consists largely of first- or second-year groups.

For example, the repopulation of Ninety Mile Beach during the last decade was almost certainly accomplished via settlement. Hefford (1945) recorded a decline in the population in 1945, and by 1948 the numbers of toheroa on the beach were so low that worthwhile estimates could not be made (Cassie 1955). Isolated groups of young toheroa were recorded from 1955 on, and a reasonable abundance in 1957 was reported (New Zealand Marine Department 1958). The Marine Department survey in July 1957 indicated the population to be 6,250,000, of which 80% were under the legal size limit (7.6 cm). This repopulation was probably due to spatfalls in 1955 to 1957. The resurgence may have been very rapid in 1961. The post-season survey indicated a population of 7,800,000; by the post-season survey of the following year it was 25,000,000, and in 1963 it was 35,000,000. Most were again under 7.6 cm long. The population can also decline as rapidly, for in 1967 there were fewer than 1,000,000 toheroa left on the beach.

Along the North Auckland west coast the degree of the population fluctuations decreases from north to south and the intensity of the spatfall is not uniform on all beaches during the same period. Often only one beach will receive a good spatfall in any year. This situation may be controlled by the apparent fluctuations that occur in the water circulation along the west coast of New Zealand. The direction of the near-shore currents may oscillate from a predominantly north-flowing system along the whole coast to a divergent system with a north-flowing component along Ninety Mile Beach and a south-flowing one along the rest of the coast towards Cape Egmont. Toheroa have been shown to be capable of spawning during most of the year, and the dispersal and subsequent settlement of the spat will be affected by these changes in the current direction.

The very successful spatfalls on Ninety Mile Beach and Dargaville beach may be caused by the spat from one beach population being reinforced by spat from another. During the first part of the peak spawning period from November to February the currents are north flowing, which would favour spatfalls on Ninety Mile Beach and Dargaville beach. Ninety Mile Beach may be fortunate that at times it could receive spat derived from all the populations along the west coast. During the latter part of the peak spawning periods the currents are divergent, which would favour Dargaville or Muriwai Beach. The regular north-flowing summer current between Reef Point and Cape Reinga may cause spat from Ninety Mile Beach to be carried along and away from the beach to settle in Doubtless Bay, which would give rise to the population on Tokerau Beach.

The poor settlement of spat on the Wellington west coast beaches may also result from persistent currents sweeping the spat away from the coast. Examination of histological sections of gonadal material from toheroa gathered at various times from these beaches suggests that the reproductive cycle is similar to that of the Dargaville population. The settlement of spat on the beach in Te Waewae Bay appears to be fairly regular from year to year, which indicates that the embayed situation produces a semi-closed circulation system.

The checks in the shells of bivalve molluscs are due to an interruption of or a change in the rate of the shell growth. Various authors have indicated that checks may be attributed to spawning, changes in the ambient temperature, or physical disturbance. The time that the checks visible in the toheroa shell are formed suggests that they may be due to the onset of the main peak of spawning from November to February. However, there is also a distinct change in the ratio of the major phytoplankters from summer

to winter. Toheroa are almost restricted to regions where the diatom *Chaetoceros armatum* T. West is plentiful in the plankton. Cassie and Cassie (1960) have shown that though *C. armatum* is present in west coast waters throughout the year, it is most abundant in winter, when dense blooms occur. The authors quote a maximum productivity value for one period in August on Waitarere Beach (Wellington west coast) of 400 mg C/(m^3h) at 300 ft-candles. This dietary change from summer to winter may cause the formation of the annual bands.

If the formation of the bands is associated with the presence of plentiful *C. armatum,* the exact time of formation of the bands may be somewhat variable. The period of the major spawning peak may be variable and the time of spawning during the year will also influence the length of an animal at the time of formation of the first band and hence each subsequent band. These factors reflect on the accuracy of the shell ageing technique as a means of determining the age-growth relationship. However, the measurement of a large number of shells with known numbers of bands has given a reasonable interpretation of the average growth of toheroa.

It is not clear at present whether the population declines are directly due to overexploitation or to natural causes. Rapson (1952) indicates that even in the nineteenth century toheroa were not always plentiful. The records also show that the stocks are capable of rapid recovery. There are some indications that mortality through natural causes may be the most important. The animal lives in an extremely unstable substrate which may be there one day and gone the next. It appears likely that large-scale movement of sand by either deposition or erosion will be the largest single cause of mortality either directly by burial too deep for survival or indirectly by leaching the animal out of the substrate so that it is more easily taken by its predators. This coupled with resurgent spatfalls would give rise to the skewed distributions characteristic of toheroa populations.

However, with the increasing popularity of the shellfish as an amateur fishery, care must be taken to ensure that the stocks are not overexploited. An increase in the size limit from 3 in. (7.6 cm) to 3.75 in. (9.5 cm) would increase the spawning potential of the animal and would also benefit the consumer, as the same number of shellfish would give substantially increased meat yields. Rapson (1952) quoted meat yields for given sizes of toheroa, and an increase in the minimum size to 9.5 cm would increase the meat yield by 75%. However, the fairly high mortality rate of 50% per year would mean that there were substantially lower numbers of toheroa to harvest at this size. It seems likely that much of this high mortality is due to natural causes.

SUMMARY

Present opinions regarding the taxonomy of the New Zealand mactracean bivalves are indicated and an account of the distribution of the toheroa is given. A history of the exploitation of the animal since 1900 is also outlined.

The physical environment and the fauna of the beach and the adjacent sub-littoral are described for Dargaville beach. Toheroa colonise the low-lying region of the littoral, where the sand is saturated during periods of low water.

Growth curves for juveniles in the first year and for adults to 7 years are presented. The legal size limit of 3 in. (7.6 cm) is attained in the third year.

A consideration of the condition and reproductive cycles indicates that the animal is capable of breeding throughout the year, with a peak of spawning during summer.

Setting is random and depends on the prevailing near-shore water circulation. Toheroa juveniles are mechanically sorted by wave action towards the high water mark and subsequently move down shore to the mean tide levels, where aggregations are formed.

The population structure is resurgent, and the survival rate is about 50% per year. Attempts to find an off-shore population were unsuccessful.

ACKNOWLEDGMENTS

I am indebted to the many people who have helped me during this study. In particular I thank Meredith Bros. and Company Ltd., who financed my fellowship, and Messrs J. K. Shea and C. W. J. Sanders for their encouragement and for the use of the company's records. I also thank Mr H. Van Kam for his assistance in the field and Mr. G. Duncan Waugh for reading this manuscript and for the support tendered by the Fisheries Research Division.

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Printed by McKenzie Thornton Cooper Ltd., 4 Nelson Street, Wellington,
by authority A. R. Shearer, Government Printer.

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